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Impressions of the Attachment of the Soft Body to the Shell in Late Cretaceous Pachydiscid Ammonites from the Western Interior of the United States

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ABSTRACT

Late Cretaceous pachydiscid ammonites *Menuites oralensis* Cobban and Kennedy, 1993 and *Menuites portlocki* (Sharpe, 1855) *complexus* (Hall and Meek, 1856) from the Western Interior of the United States show four kinds of markings on the phragmocone and body chamber. These markings are preserved on internal molds that retain traces of the original shell, mostly the inner prismatic layer.

(1) *Transverse lines* appear on the surface of the inner prismatic layer and extend adorally as far as midway onto the adult body chamber. They consist of a sequence of regularly spaced iridescent lines that usually cross the venter with a marked adoral projection, forming a chevronlike pattern. The transverse lines do not follow the shape of the apertural margin. Viewed in close-up, these lines appear as narrow bands of nacre; the adoral edge of each band is ragged and the adapical edge thins out and disappears.

(2) A *longitudinal band* occurs on the flanks and extends from the umbilicus to about two-thirds whorl height. It appears on the surface of the inner prismatic layer.

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(3) A *mid-ventral band* extends for several tens of millimeters adoral of the ultimate septum and terminates in an unpaired scar. It appears on the internal mold and is visible below the inner prismatic layer.

(4) A *pair of dorsal scars* occurs on the internal mold several millimeters adoral of the ultimate septum. Each scar is boomerang-shaped and extends from the dorsal margin to just ventral of the umbilical shoulder.

We hypothesize that the transverse lines formed at the adapical margin of the zone of nacreous secretion in the middle of the body chamber. They may have represented narrow bands of mantle attachment. The longitudinal band demarcated a broad area of nacreous secretion on the flanks, which may have represented an additional area of mantle attachment. During growth, both the transverse lines and the longitudinal band were overlain by the inner prismatic layer (and are thus now visible on the surface of this layer on partially exfoliated shells). The mid-ventral scar and dorsal scars just adoral of the ultimate septum are the sites of attachment of the soft body at the adapical end of the body chamber. These sites developed on the inside surface of the inner prismatic layer (and are thus now visible on the internal mold below the inner prismatic layer, if present).

INTRODUCTION

The attachment of the soft body to the inside surface of the shell in ammonites was first discussed by Crick (1898) and this subject has been extensively reviewed by Doguzhaeva and Mutvei (1996). Such studies rely on very well-preserved material and reveal a variety of attachment patterns. We describe markings on the internal molds of pachydiscid ammonites, which we interpret as sites of soft body attachment. One of us (S.D.J.) first observed these markings on specimens of *Menuites oralensis* (Cobban and Kennedy, 1993) from the Late Cretaceous (Campanian) Pierre Shale of South Dakota.

There are four kinds of markings: (1) Transverse lines occur on a thin layer of shell covering the internal mold. They display a chevronlike pattern on the venter; they do not follow the course of the growth lines. (2) A longitudinal band runs along the flanks and extends from the umbilicus to about two-thirds to three-quarters whorl height. It demarcates an area of nacreous shell secretion. (3) A mid-ventral band occurs on the internal mold slightly adoral of the ultimate septum and terminates in some specimens in an unpaired muscle scar. (4) A pair of dorsal scars appears on the internal mold slightly adoral of the ultimate septum.

The specimens described in this paper are deposited in one of four collections: the American Museum of Natural History, New York, New York (AMNH); the U.S. National Museum, Washington, D.C. (USNM); the Black Hills Museum of Natural History, Hill City, South Dakota (BHMNH); and the private collection of Steven D. Jorgensen, Omaha, Nebraska (indicated by An or Me and a three or four digit number).

MATERIALS AND METHODS

We studied approximately 40 specimens of *Menuites oralensis* from the Upper Cretaceous (Campanian) of the U.S. Western Interior, approximately 25 of which showed markings and 19 of which are illustrated. They are from the *Baculites scotti* Zone of the Pierre Shale in South Dakota, Wyoming, and Colorado.

The specimens can be subdivided into microconchs, macroconchs, and juveniles and range from 28 to 167 mm in diameter. They include parts of phragmocones or body chambers or phragmocones with partial to nearly complete body chambers. The diameter (D) of unbroken specimens is given in parentheses in the description of each specimen. The specimens are internal molds with portions of the shell wall preserved as the original aragonite. In many specimens, a thin layer of transparent shell (the inner prismatic layer) covers part or most of the internal mold (fig. 1A).

Menuites oralensis is characterized by a subglobose to subquadrate, moderately involute shell and is strongly dimorphic. Microconchs range in diameter from 30 to 65 mm (Cobban and Kennedy, 1993). They have stout whorls that are broadest at the umbilical shoulder. The flanks are broadly

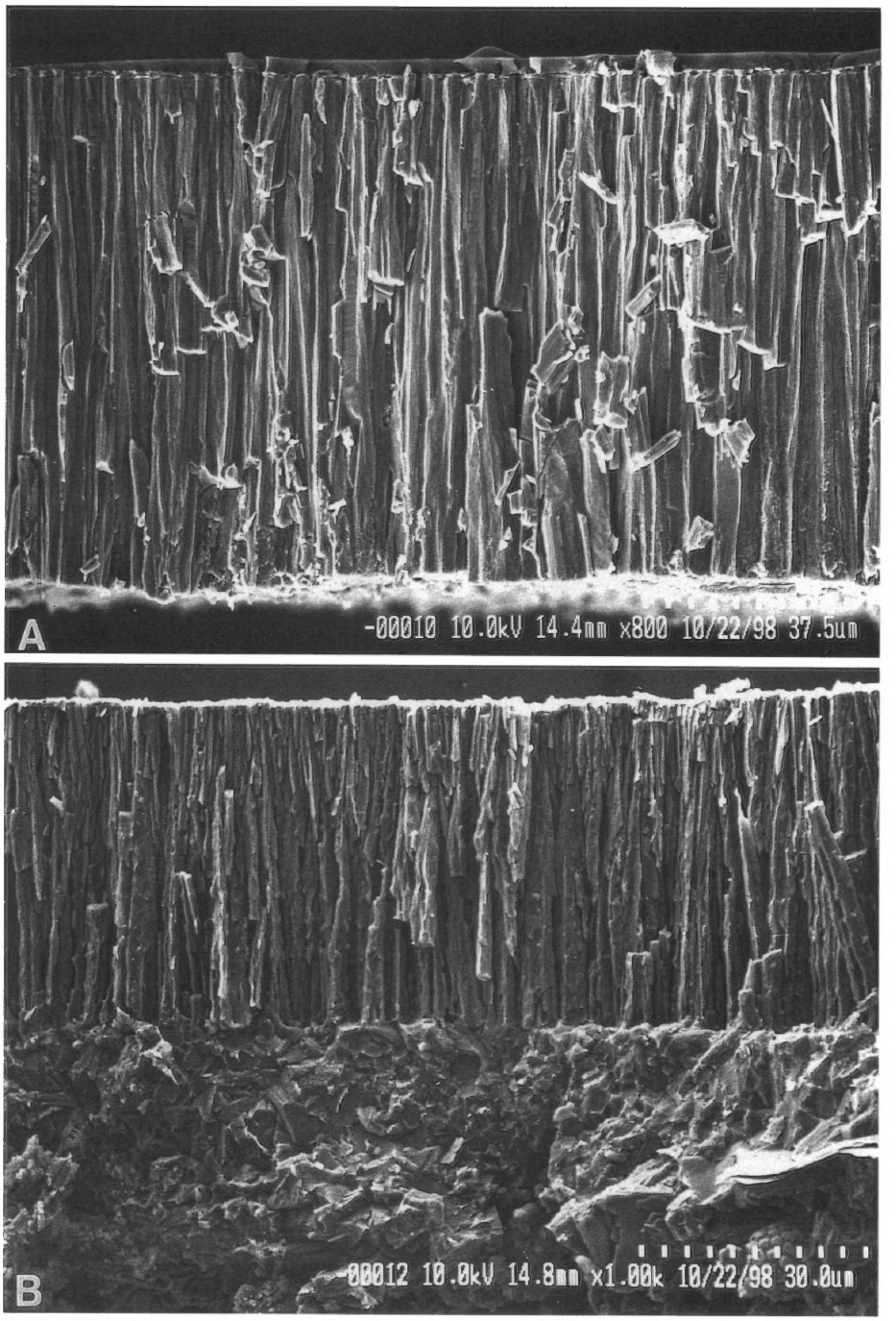

Fig. 1. *Menuites oralensis* Cobban and Kennedy, 1993, *Baculites scotti* Zone, South Dakota. **A.** Microstructure of the inner prismatic layer that covers the surface of the internal mold in BHMNH 4811. Scale indication = 37.5 μm. **B.** Microstructure of the mid-ventral band in USNM 506951. The material in the bottom half of the photo is the internal mold itself. Scale indication = 30 μm.

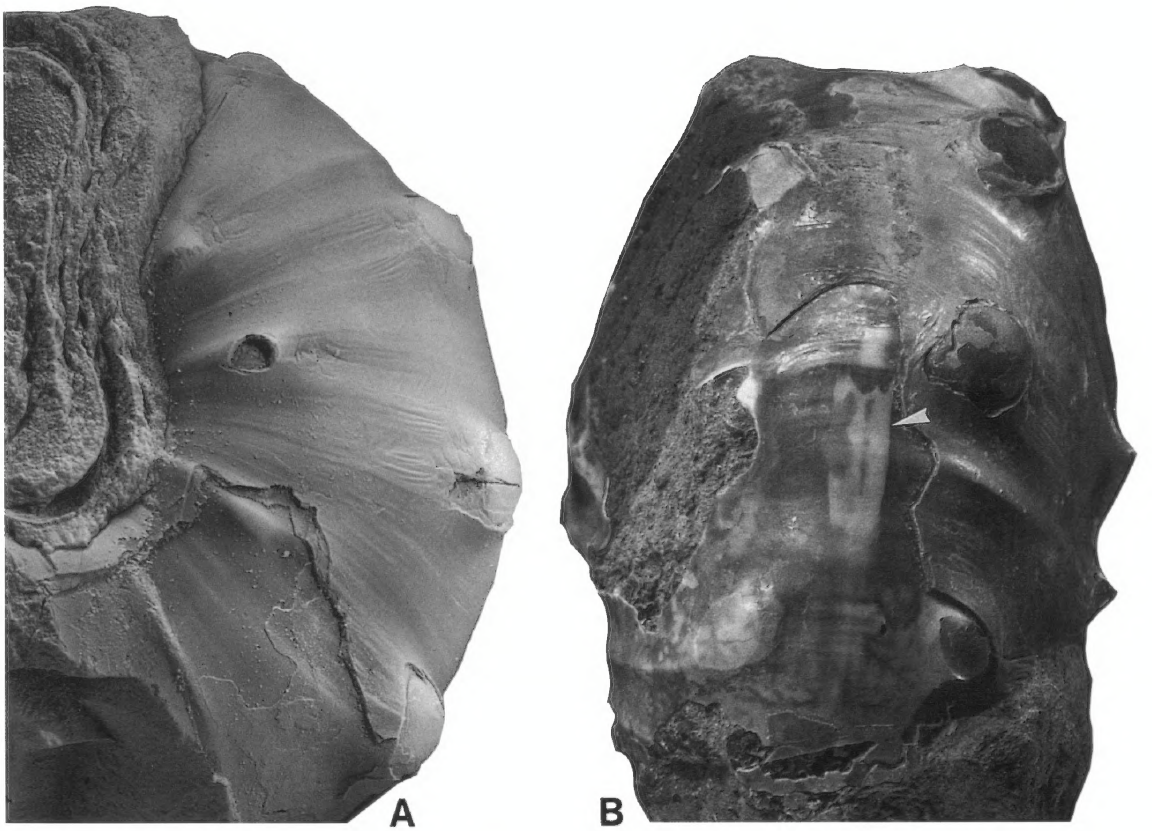

Fig. 2. *Menuites oralensis* Cobban and Kennedy, 1993, USNM 506949, a small microconch (D = 67.7 mm), *Baculites scotti* Zone, Pierre Shale, South Dakota. **A.** Left lateral view of part of the body chamber showing the growth lines, which are weakly convex on the flanks. Adoral direction is toward bottom of photo. Coated, ×1.3. **B.** Ventral view of the adapical part of the body chamber (uncoated) showing the mid-ventral band (arrow) below a thin layer of transparent shell (the inner prismatic layer). The band ends abruptly in a sharp, irregular margin but a narrower band continues for several millimeters more before it is covered by a thick layer of shell. Adoral direction is toward top of photo. Approximately ×1.75.

rounded and the venter is more narrowly rounded. Umbilical bullae appear on the early whorls but disappear midway on the adult body chamber. Ribs also appear on the early whorls but weaken or disappear on the adapical part of the adult body chamber; they rejuvenate near the adult aperture. Ribs are prorsiradiate on the flanks and cross the venter with a broad convexity. Five to seven pairs of ventrolateral nodes develop on the adoral part of the phragmocone and adapical part of the adult body chamber, and then abruptly disappear. The body chamber consists of approximately one-half to two-thirds of a whorl. The apertural margin follows the course of the ribs.

Macroconchs are more compressed and larger than microconchs, but the ornament of the early whorls is the same in both dimorphs (Cobban and Kennedy, 1993). However, in macroconchs, the umbilical bullae disappear at a shell diameter of 60–90 mm and the ribs disappear at a shell diameter of 90–100 mm. By about 110 mm, the shell is smooth except for growth lines, and the flanks are flattened. The body chamber consists of approximately two-thirds of a whorl.

The pattern of growth lines is the same in both macroconchs and microconchs (fig. 2A). The growth lines are rursiradiate on the umbilical wall. They swing slightly forward at the umbilical shoulder and are weakly con-

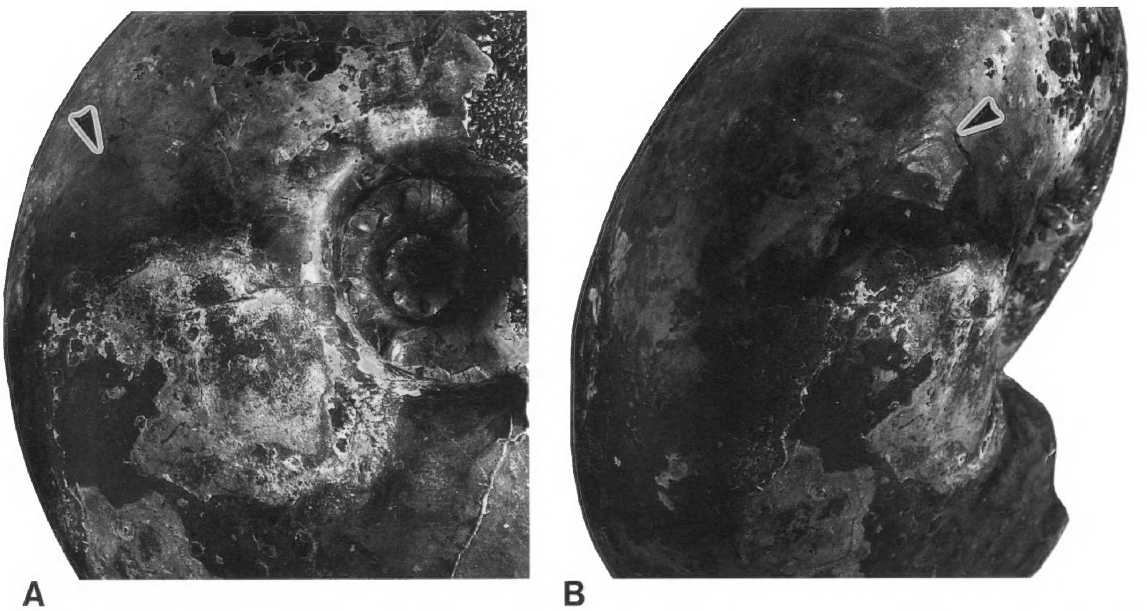

Fig. 3. *Menuites oralensis* Cobban and Kennedy, 1993, AMNH 46004, a large adult macroconch with a nearly complete body chamber (D = 164 mm), *Baculites scotti* Zone, Pierre Shale, South Dakota. The specimen is an internal mold; except for the last quarter whorl, it is covered by the inner prismatic layer. **(A)** right lateral view, **(B)** three-quarter view of the middle part of the body chamber. The arrows indicate a sequence of transverse lines on the outer flanks and ventrolateral margin. ×0.75.

vex on the flanks. They bend forward again on the outer flanks and cross the venter with a broad convexity.

In addition to *Menuites oralensis,* we studied 10 specimens of *Menuites portlocki* (Sharpe, 1855) *complexus* (Hall and Meek, 1856) from the Upper Cretaceous (Campanian) of the U.S. Western Interior, five specimens of which showed similar markings to those on *M. oralensis* (none illustrated). This species differs from *M. oralensis* in having stronger and more widely spaced ribs on the early whorls. The specimens are from the *Baculites gregoryensis* Zone of the Pierre Shale in central South Dakota and Colorado and the *B. reduncus* Zone in Wyoming and southwestern South Dakota. They are internal molds although a few retain traces of the original aragonitic shell.

There is one specimen in our collections (An1086A) from the *Baculites scotti* Zone that does not match any of the previously described specimens of *Menuites oralensis* or *Menuites portlocki complexus.* It is a large compressed phragmocone, 164 mm in diameter, with weak, closely spaced ribs on the early whorls, which flatten out and disappear on the later whorls, leaving a nearly smooth shell surface. Only the left side of the specimen is preserved and retains portions of the original aragonitic shell. We have tentatively identified this specimen as *Pachydiscus* (*Pachydiscus*) cf. *catarinae* Anderson and Hanna, 1935.

To observe the markings on the shells, specimens were viewed at various angles under incident illumination. Smaller specimens were examined with a microscope. The inside surface of the shell wall was examined with scanning electron microscopy.

TRANSVERSE LINES

Observations

The best set of transverse lines occurs on AMNH 46004 (figs. 3–5), an internal mold of a large macroconch with two-thirds whorl body chamber (D = 164 mm). The lines are iridescent and each is approximately 0.5–1 mm wide on the mid-venter. They occur on a thin layer of transparent shell (the inner prismatic layer) that covers most of the in-

Fig. 4. *Menuites oralensis* Cobban and Kennedy, 1993, AMNH 46004 (specimen in fig. 3). Ventral view of the middle part of the body chamber. The transverse lines cross the venter with a marked adoral projection, forming a chevronlike pattern (arrow). ×0.85.

ternal mold. They are present on both sides of the middle part of the body chamber. The transverse lines show a different pattern than that of the growth lines. They are sinuous on the umbilical wall and flanks, forming a series of undulations that increase in amplitude toward the venter. The lines sweep backward and sharply forward on the outer third of the flanks, producing a large concavity. They intersect the ventrolateral margin at an acute angle and cross the venter with a sharp adoral projection. The lines form a chevronlike pattern and are regularly spaced at intervals of 3–6 mm on the mid-venter.

Closely spaced transverse lines are visible on USNM 506946, a body chamber of an adult microconch (D = 78.4 mm) (fig. 6A). They appear near the base of the body chamber on the umbilical wall and inner flanks. Each line is approximately 0.5 mm wide. The lines occur on a very thin layer of transparent shell (the inner prismatic layer) that is approximately 150 μm thick.

In USNM 506947, a juvenile with part of the body chamber preserved (D = 27.4 mm), transverse lines are conspicuous on the adoral part of the phragmocone and adapical part of the body chamber (fig. 6B). The lines are iridescent and occur on the surface of a thin layer of transparent shell. The adoral edge of each band is ragged and approximately 20 μm thick; the adapical edge feathers out and disappears. The lines originate at the umbilical seam, and are convex and closely spaced on the umbilical wall (2 or 3 lines/mm). Four lines are visible on the flanks and venter; they swing sharply forward at the umbilical shoulder and form a broad adoral projection on the venter.

In BHMNH 4923, an adult microconch (D = 93.0 mm), there are numerous transverse lines on the right side of the body chamber (fig. 7A–C). They appear on the surface of a thin layer of transparent shell and are characterized by ragged adoral edges and more even adapical edges. They are spaced at intervals of 0.5 mm on the umbilical shoulder; each line is approximately 0.1 mm wide. The lines are slightly prorsiradiate on the umbilical wall. They are weakly convex on the umbilical shoulder and weakly concave on the innermost flanks. They sweep markedly forward on the middle to outer flanks and cross the venter with a sharp adoral projection. In one area near the ventrolateral shoulder there are six closely spaced lines. The most adoral lines appear one-third of the way into the body chamber.

BHMNH 2065, a partial body chamber of a microconch, shows three transverse lines on the left side of the body chamber (fig. 6D). The lines are strongly prorsiradiate on the inner flanks and then abruptly become rectiradiate on the mid-flanks, before fading out. Each line is iridescent and approximate-

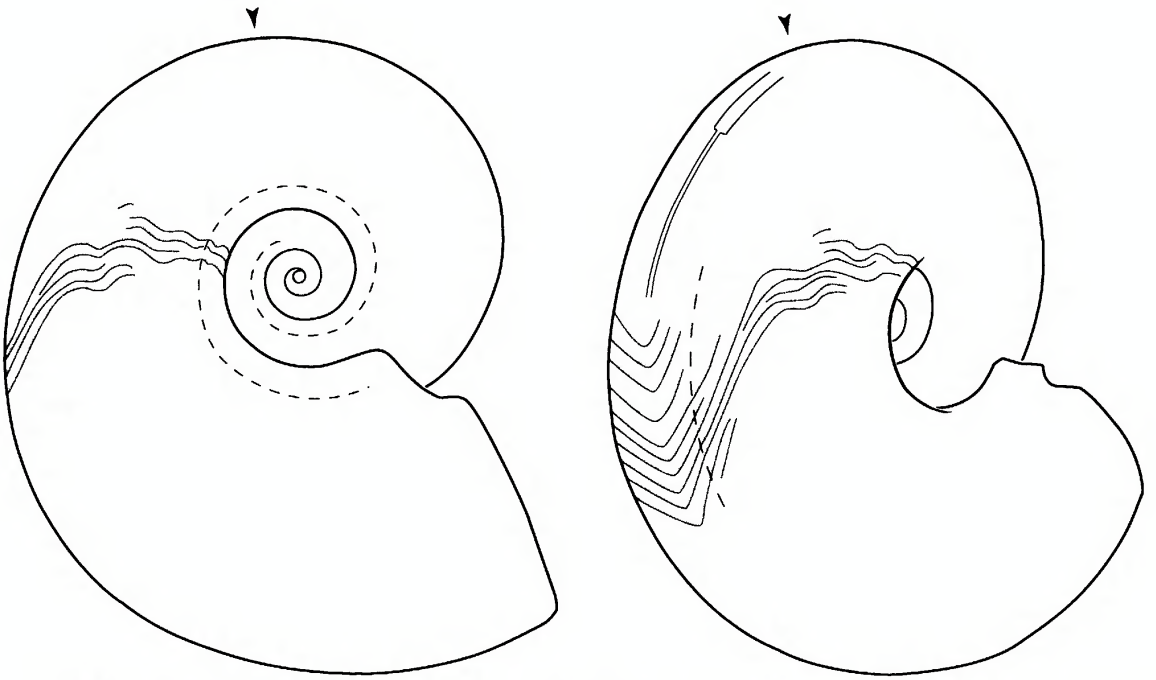

Fig. 5. *Menuites oralensis* Cobban and Kennedy, 1993, AMNH 46004 (diagrams of specimen in figs. 3, 4). Right lateral (left) and three quarter view (right) showing several transverse lines and the mid-ventral band. The lines are sinuous on the umbilical wall and flanks, forming a series of undulations that increase in amplitude toward the venter. The lines cross the venter with a sharp adoral projection. The dashed lines represent the umbilical shoulder and the ventrolateral margin. Arrows indicate base of body chamber. ×0.50.

ly 0.25 mm wide. The lines occur on the surface of a thin layer of transparent shell. The adoral edge of each line is steep and ragged. This specimen also shows several transverse lines on the venter on the left side of the midline. They occur adoral of a shell pathology that is expressed as two longitudinal ridges, each 5 mm long. The transverse lines on the venter form a series of chevrons that point in an adapical direction, unlike the chevrons in other specimens. The transverse lines swing backward just right of the midline, after which they disappear.

In USNM 456691, a microconch (D = 87.7 mm), several lines are visible on the flanks on the adapical third of the body chamber (figs. 6C, 8). The lines are concave on the inner flanks and broadly convex on the outer flanks. They are spaced at intervals of approximately 1 mm on the ventrolateral margin. They appear on the surface of a thin layer of shell (the inner prismatic layer). The adoral edge of each band is ragged and approximately 20 μm thick. The band decreases in thickness in an adapical direction. As a result, the adapical edge of each band usually feathers out. When the bands are closely spaced, they form a series of imbricated cuestas, with each adapical band lying on top of the next most adoral band.

Transverse lines are also visible on the inside surface of the shell wall of this specimen (fig. 9). At low magnifications (50×, 200×), the transverse lines appear as narrow, sinuous bands approximately 50 μm wide. They have a rougher texture and lighter "color" than the surrounding shell. At higher magnifications (1000×), the nacreous layers of the shell are visible. The prismatic layer is absent (it is preserved instead on the internal mold). The adoral edge of each band ends in an abrupt elevation, adapical of which many nacreous layers have spalled off. The adapical edge of each band is marked in places by a ridge of stacked-up nacreous crystals. Pores are present in the nacre. The pores are

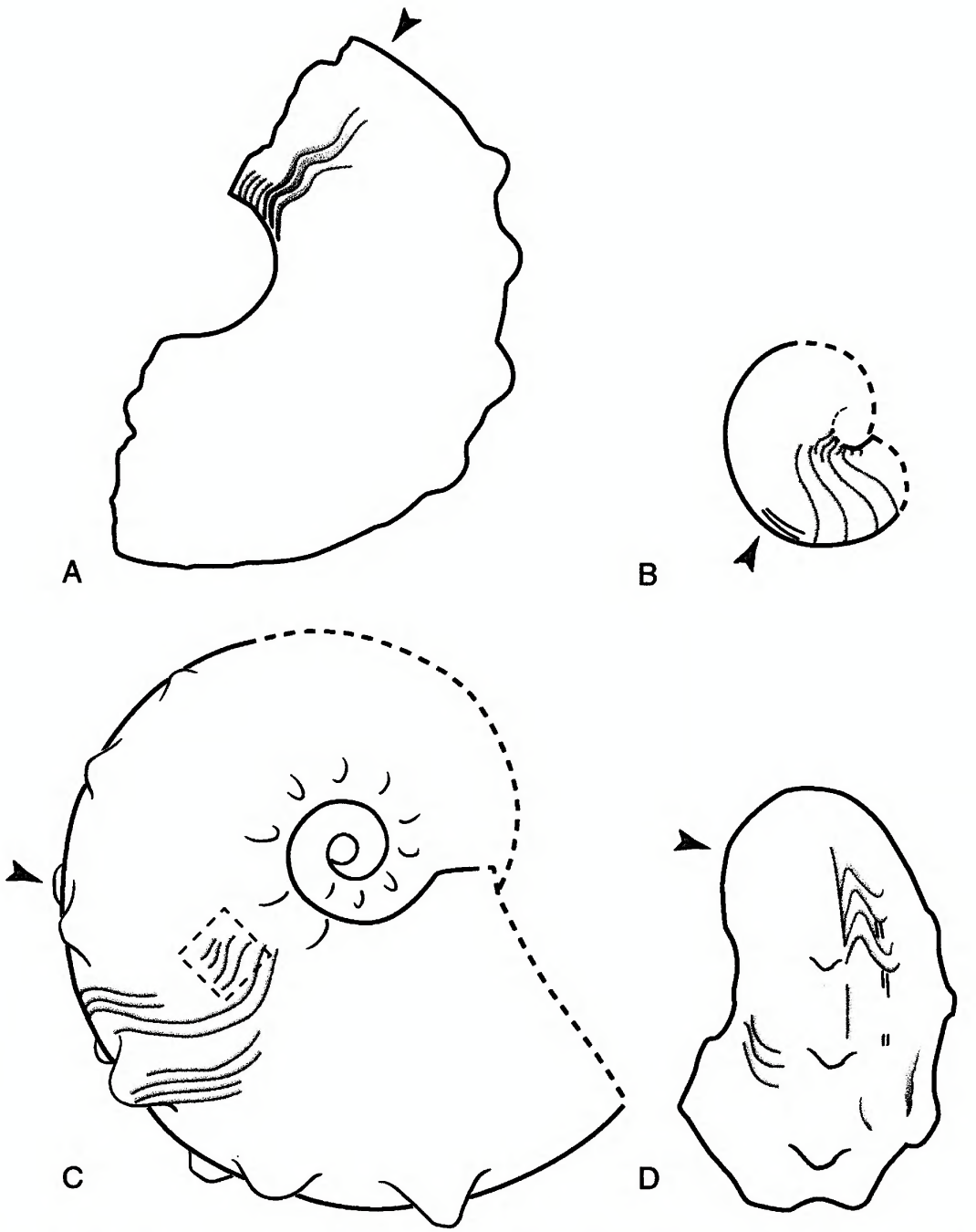

Fig. 6. Diagrams of *Menuites oralensis* Cobban and Kennedy, 1993, *Baculites scotti* Zone, Pierre Shale, South Dakota. Arrows indicate base of body chamber. **A.** Left lateral view of USNM 506946, a partial body chamber of an adult microconch (D = 78.4 mm). The specimen is an internal mold, most of which is covered by the inner prismatic layer. The transverse lines are visible on the umbilical wall and inner flanks. **B.** Three-quarter view of USNM 506947, a juvenile (D = 27.4 mm). The specimen is an internal mold, most of which is covered by the inner prismatic layer. Several transverse lines are visible on the body chamber. **C.** Right lateral view of USNM 456691, an adult microconch with a nearly complete body chamber (D = 87.7 mm). The specimen is an internal mold; except for the last fifth whorl, it is covered by the inner prismatic layer. Some parts of the specimen also retain substantial

approximately 1 μm in diameter and occur with equal frequency on the bands and on either side of them.

Several other specimens show transverse lines. An389D, a macroconch (D = 101.2 mm), shows transverse lines on the phragmocone (fig. 10B). They occur on the venter just adapical of the base of the body chamber. A few lines are present on the venter of the body chamber of Me1088, a microconch (D = 66.3 mm) (figs. 10A, 11). They occur on a thin layer of shell that is transparent in some places and nearly opaque in others. In Me791, a microconch, four transverse lines occur on the adapical part of the body chamber near the ventrolateral margin (fig. 10C). They are spaced at distances of approximately 1 mm. (See figs. 10D, 12B, and 12D, for other specimens showing transverse lines.) Transverse lines also occur in association with the longitudinal band (see below).

Summary

The transverse lines appear on both the phragmocone and the body chamber where they are confined to the posterior half. This is especially apparent in specimens with nearly complete body chambers like AMNH 46004.

The transverse lines originate at the umbilical seam. They are sinuous and prorsiradiate on the flanks and cross the venter with a fairly sharp adoral projection, forming a series of chevrons. There is an ontogenetic change in the shape of the transverse lines in that the adoral projection on the venter is much more pronounced in adults than in juveniles (compare AMNH 46004 with USNM 506947). The shape of the lines is also subject to change due to pathology, as shown in BHMNH 2065, in which the chevrons point in an adapical rather than adoral direction, adoral of a shell injury. In addition, there is taxonomic variation in the shape of the lines at the generic level (see the description of An1086A, a specimen of *Pachydiscus* (*Pachydiscus*) cf. *catarinae*).

The transverse lines do not follow the shape of the apertural margin as inferred from the ribs and growth lines. The growth lines are weakly sinuous on the flanks (where the shell wall is preserved), whereas the transverse lines are very sinuous. Similarly, none of the ribs or growth lines shows the marked adoral projection on the venter characteristic of the transverse lines.

One of the most notable features of the transverse lines is that they are fairly regularly and closely spaced. For example, in AMNH 46004, the lines are spaced at distances of 3–6 mm on the mid-venter. The distance between lines is much smaller than that between septa.

The transverse lines occur on a thin layer of transparent shell, the inner prismatic layer, which is approximately 150 μm thick. Viewed in close-up, the lines appear as thin, narrow bands of iridescent nacre, approximately 20 μm thick and 0.1–1 mm wide. They decrease in thickness adapically. The adoral edge of each band is steep and ragged and the adapical edge feathers out and disappears. When the bands are closely spaced, they form a series of imbricated cuestas, with each adapical band lying on top of the next most adoral band. The effect is that of descending a staircase in an adoral direction.

On the inside surface of the shell wall, the transverse lines appear as narrow bands in the nacreous layer. Each band represents a zone of plucked nacre (which is actually what is preserved on the internal mold). The adoral edge of a band is more distinct than the adapical edge. On either side of a band, the shell surface is relatively smooth nacre. However, both the bands and the adjacent shell surfaces show pores.

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pieces of shell wall. The transverse lines are visible on the flanks and venter. The square marks the area where we examined the inside surface of the shell wall. The umbilical bullae are shown in the drawing. **D.** Three-quarter view of BHMNH 2065, a partial body chamber of a microconch. It is an internal mold, the initial two-thirds of which are covered by the inner prismatic layer. The transverse lines on the venter form a series of chevrons that point in an adapical direction. All approximately natural size.

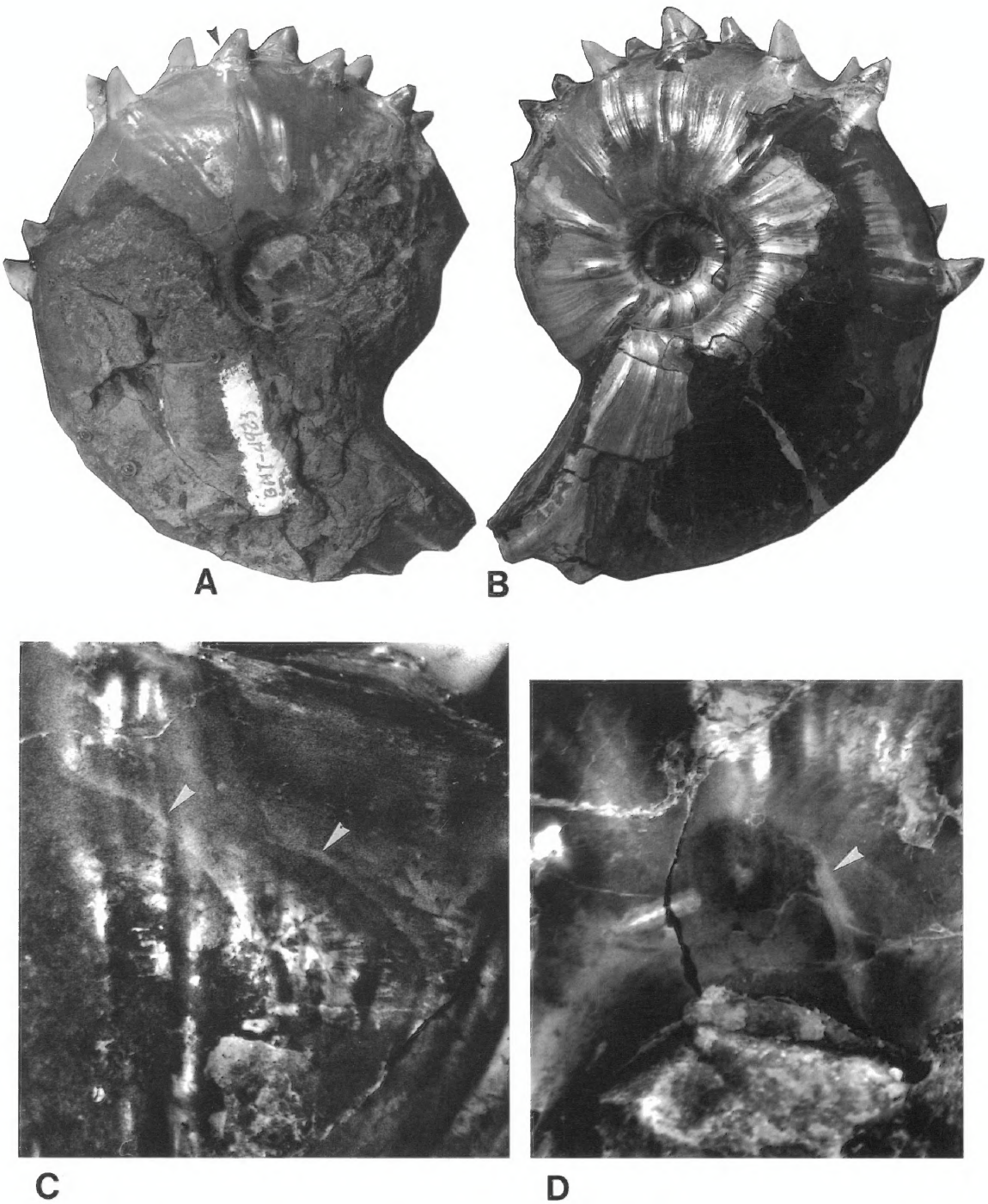

Fig. 7. *Menuites oralensis* Cobban and Kennedy, 1993, BHMNH 4923, an adult microconch (D = 93.0 mm), *Baculites scotti* Zone, South Dakota. **A.** Right lateral view, uncoated, ~×1. Arrow indicates base of body chamber. **B.** Left lateral view showing the prominent ventrolateral spines that are only preserved as nodes in most specimens. Uncoated, ~×1. **C.** Close-up of the transverse lines (arrows) on the right side of the body chamber near the ventrolateral margin (note the ventrolateral spine at top of photo). The lines cross the venter with a sharp adoral projection toward the left of the photo. ~×4. **D.** Close-up of part of the dorsal muscle scar (arrow) on the right side of the body chamber. It is preserved as a cream-colored transverse band on the umbilical wall. Adoral direction is toward left of photo. ~×4.

Fig. 8. Right lateral view of *Menuites oralensis* Cobban and Kennedy, 1993, USNM 456691, an adult microconch, *Baculites scotti* Zone, Pierre Shale, South Dakota (specimen in fig. 6C). Outside arrow indicates base of body chamber. Several transverse lines are visible on the outer flanks near the ventrolateral margin (arrow). Approximately ×0.90.

LONGITUDINAL BAND (LINE)

OBSERVATIONS

In USNM 456679 (figs. 12A, 13), a body chamber of a small macroconch (D = 84.4 mm), there is a longitudinal band on the right side of the specimen that extends from the umbilicus to two-thirds whorl height. It is iridescent and lies on the surface of a thin layer of transparent shell (the inner prismatic layer). The ventral margin of the band is visible on the adoral part of the specimen. The ventral edge of this margin is even and feathers out, whereas the dorsal edge is broken and irregular. The band is more extensive on the rest of the specimen. A series of transverse lines occurs on the flanks. The lines are concave and join the ventral margin of the longitudinal band almost asymptotically. Some of the lines are broad, approximately 1 mm wide. They are iridescent, occur on the inner prismatic layer, and have ragged adoral edges and feather-thin adapical edges. Most of the lines lie below the margin of the longitudinal band in terms of elevation; however, one transverse line is thicker and passes smoothly into the longitudinal band. Three transverse lines also appear on the ventral side of the longitudinal band on the adapical

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Fig. 9. *Menuites oralensis* Cobban and Kennedy, 1993, USNM 456691, *Baculites scotti* Zone, Pierre Shale, South Dakota (specimen in figs. 6C, 8). Scanning electron micrographs of the inside surface of a fragment of shell wall showing transverse lines. Adoral direction is toward bottom of page. **A.** The arrows indicate transverse lines. The letters mark the sites of the next photos. Scale bar = 200 μm. **B.** Close-up of a transverse line. The letters mark the sites of the next photos. Scale bar = 50 μm. **C, D, E.** Each transverse line is actually a band of plucked nacre, approximately 50 μm wide. Scale bar = 10 μm. **F.** The nacre exhibits small pores approximately 1 μm in diameter. Scale bar = 2 μm.

Fig. 10. Diagrams of *Menuites oralensis* Cobban and Kennedy, 1993, *Baculites scotti* Zone, Pierre Shale, South Dakota. Arrows indicate base of body chamber. **A.** Three-quarter view of Me1088, an adult microconch with a partial body chamber (D = 66.3 mm). The specimen is an internal mold, most of which is covered by the inner prismatic layer. Several transverse lines and the mid-ventral band are visible on the venter. **B.** Three-quarter view of An389D, a small macroconch with a nearly complete body chamber (D = 101.2 mm). The specimen is an internal mold, most of which is covered by the inner prismatic layer. Several transverse lines and the mid-ventral band are visible on the venter on the adoral part of the phragmocone. **C.** Three-quarter view of Me791, a partial body chamber of an adult microconch. The dashes represent the missing phragmocone. The specimen is an internal mold, most of which is covered by the inner prismatic layer. Several transverse lines and the mid-ventral band are visible on the venter. **D.** Three-quarter view of AMNH 46489, a partial body chamber of an adult microconch. The dashes represent the missing phragmocone. The specimen is an internal mold, most of which is covered by the inner prismatic layer. Several transverse lines and the mid-ventral band are visible on the venter. All diagrams approximately natural size.

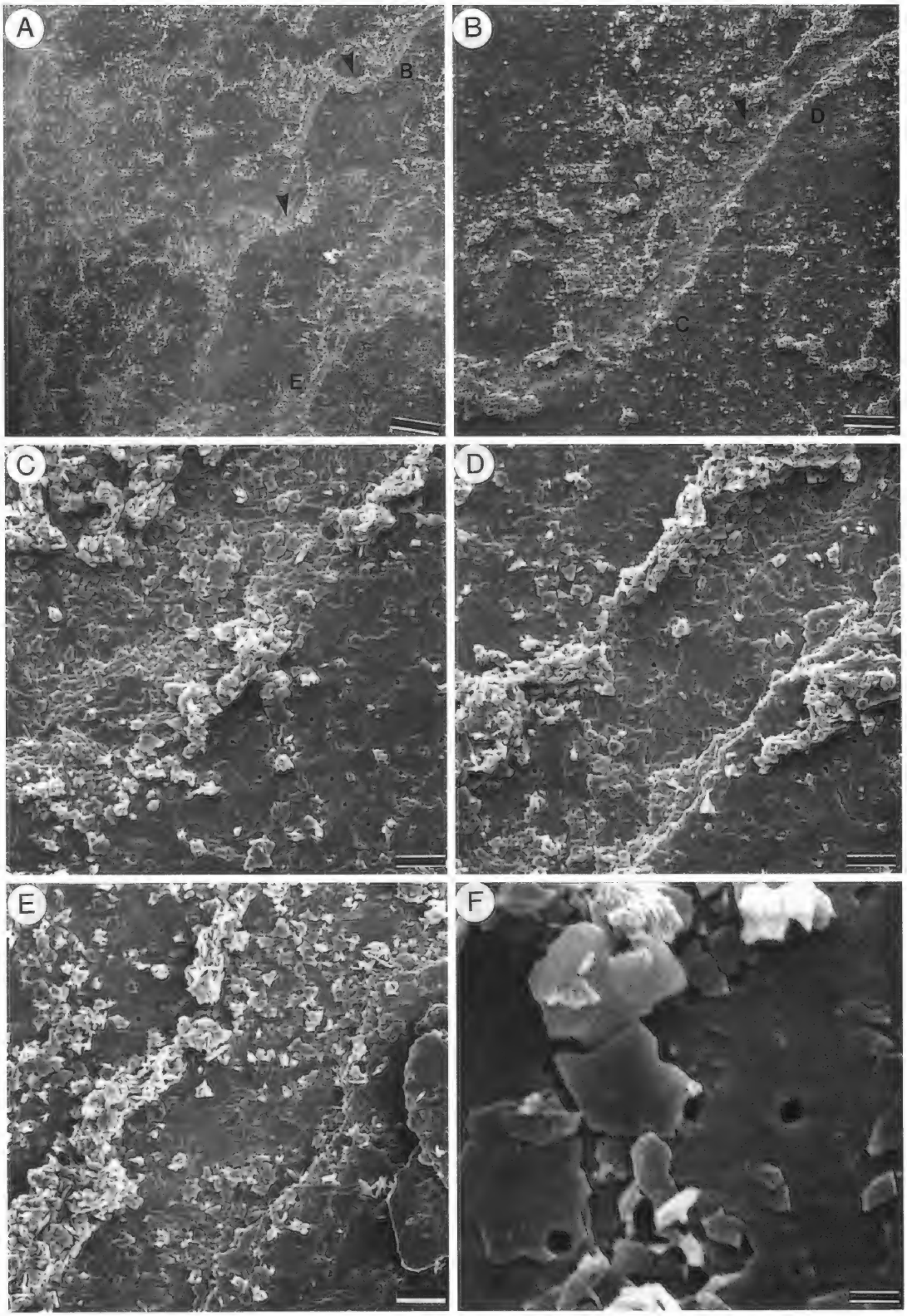

Fig. 9.

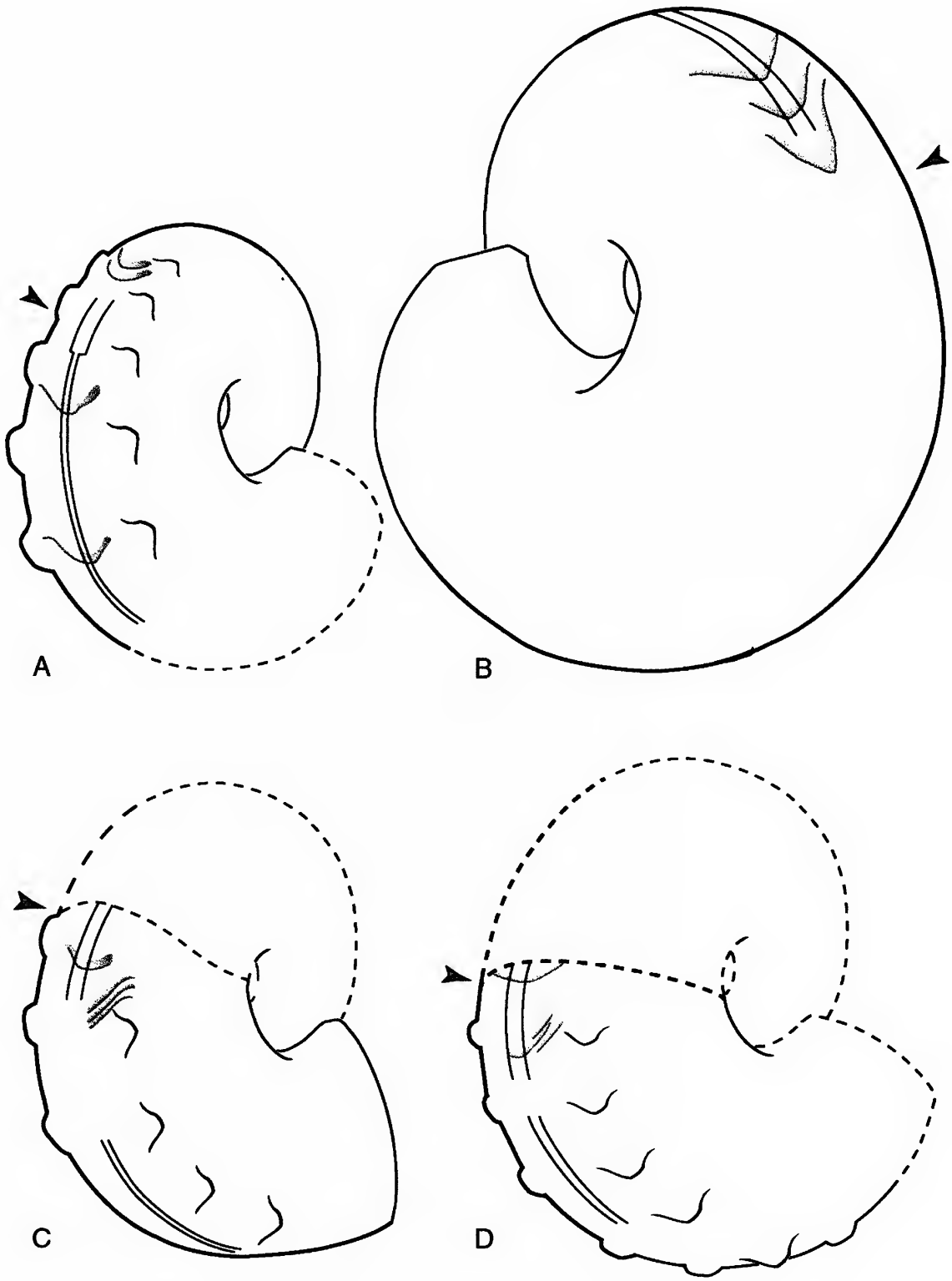

Fig. 10.

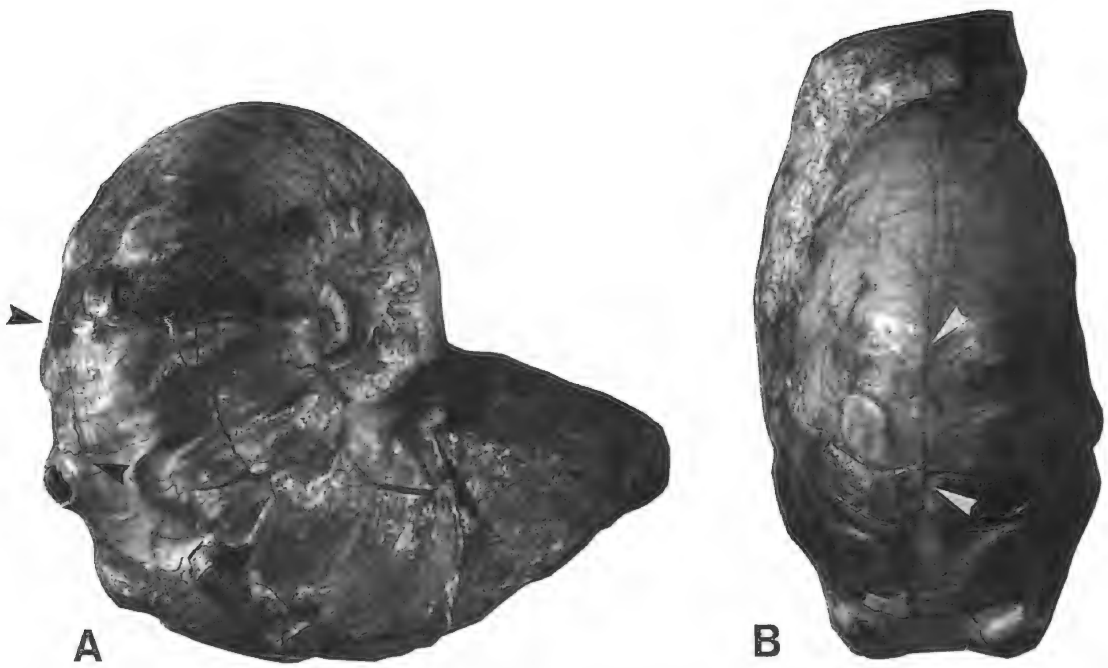

Fig. 11. *Menuites oralensis* Cobban and Kennedy, 1993, Me1088, an adult microconch with a partial body chamber, *Baculites scotti* Zone, Pierre Shale, South Dakota (specimen in fig. 10A). The specimen is an internal mold, most of which is covered by the inner prismatic layer. Outside arrow indicates base of body chamber. **A.** Three-quarter view. The lower arrow indicates the mid-ventral band. **B.** Ventral view. Upper arrow indicates a transverse line; lower arrow indicates the mid-ventral band adoral of the ultimate septum. Approximately natural size.

portion of the specimen. They have ragged adoral edges and thin adapical edges and pass smoothly into the longitudinal band.

BHMNH 4811, a small macroconch (D = 70.0 mm), shows a band of iridescent shell that extends from the umbilicus to two-thirds whorl height on the phragmocone and body chamber (this specimen also bears complicated traces of worm tubes) (figs. 12C, 14). The band occurs on a thin layer of transparent shell, the inner prismatic layer, approximately 100 μm thick. On the adapical part

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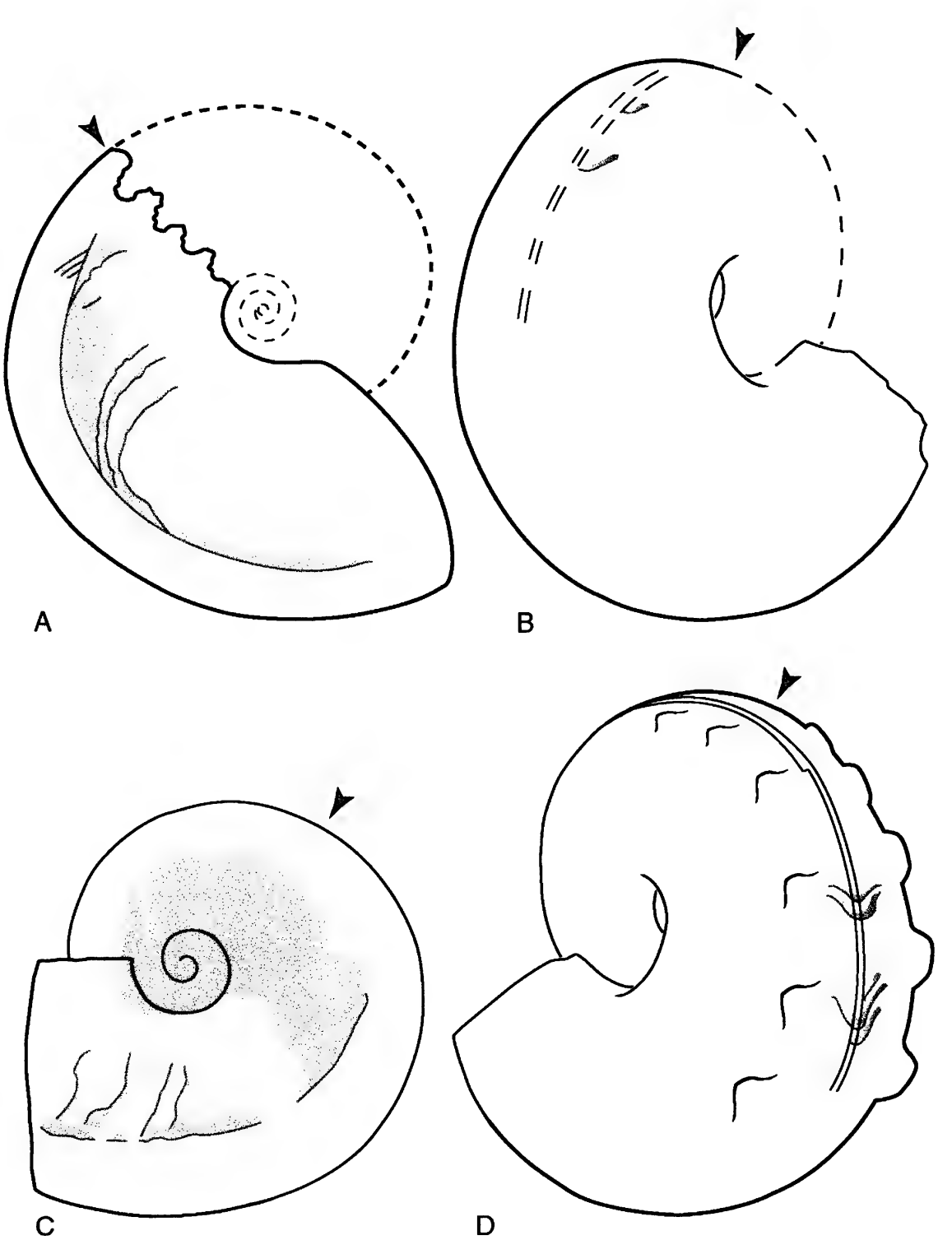
Fig. 12. Diagrams of *Menuites oralensis* Cobban and Kennedy, 1993, *Baculites scotti* Zone, Pierre Shale, South Dakota. Arrows indicate base of body chamber. **A.** Right lateral view of USNM 456679, a body chamber of a small macroconch (D = 84.4 mm). The dashes represent the missing phragmocone. The specimen is an internal mold, most of which is covered by the inner prismatic layer. The longitudinal band (shaded area) is visible on the flanks. **B.** Three-quarter view of USNM 506950, a small macroconch with a nearly complete body chamber (D = 87.8 mm). The dashes represent the missing phragmocone. The specimen is an internal mold, most of which is covered by the inner prismatic layer. Several transverse lines and the mid-ventral band are visible on the venter. **C.** Left lateral view of BHMNH 4811, a small macroconch with a partial body chamber (D = 70.0 mm). The specimen is an internal mold, most of which is covered by the inner prismatic layer (see fig. 1A). The longitudinal band (shaded area) is visible on the flanks. The band consists of a series of stacked nacreous layers on the phragmocone and adapical part of the body chamber. **D.** Three-quarter view of Me590A, an adult microconch (D = 88.4 mm). The specimen is an internal mold, most of which is covered by the inner prismatic layer. Several faint transverse lines and the mid-ventral band are visible on the venter. All diagrams approximately natural size.


A
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C
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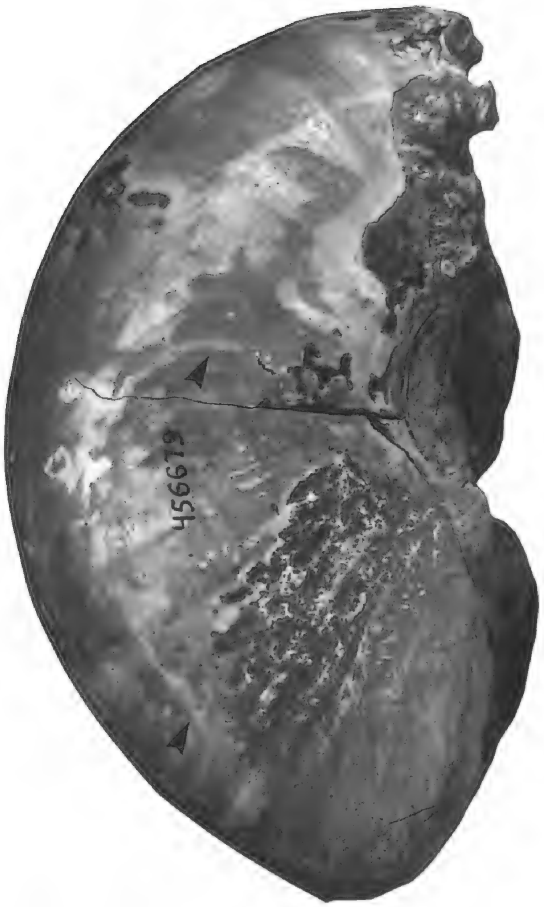

Fig. 13. Right lateral view of *Menuites oralensis* Cobban and Kennedy, 1993, USNM 456679, a body chamber of a small macroconch, *Baculites scotti* Zone, Pierre Shale, South Dakota (specimen in fig. 12A). The ventral margin of the longitudinal band is visible (lower arrow). Several transverse lines occur on the flanks (upper arrow) and join the margin of the longitudinal band almost asymptotically. Adoral direction is toward bottom of photo. Approximately ×1.4.

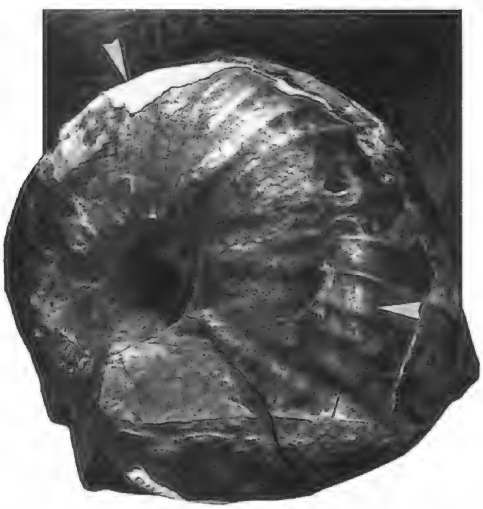

Fig. 14. *Menuites oralensis* Cobban and Kennedy, 1993, BHMNH 4811, a small macroconch with a partial body chamber, *Baculites scotti* Zone, Pierre Shale, South Dakota (specimen in figs. 1A, 12C). Left lateral view showing the longitudinal band (lower arrow). The specimen is an internal mold, most of which is covered by the inner prismatic layer. Some parts of the specimen also retain nearly complete pieces of shell wall. Arrow on top indicates base of body chamber. Approximately natural size.

of the body chamber and phragmocone the band consists of a series of stacked nacreous layers that increase in number toward the dorsum. On the adoral part of the body chamber, only the ventral margin of the band is preserved. It is 0.5 mm wide and consists of three narrow iridescent lines with two thinner, darker, matrix-colored lines, in between them. The ventral edge of the ventral margin feathers out and disappears but its dorsal edge is thicker and more ragged. There are patches of iridescent shell on the dorsal side of the ventral margin.

We also examined two specimens that are phragmocones. In USNM 506948, a phragmocone of a macroconch (D = 114.0 mm) with a variable number of shell layers still attached, there is a nearly continuous longitudinal line on the ventrolateral margin on each side of the specimen (figs. 15, 16). Each longitudinal line has a ragged dorsal edge. A fairly uniformly thick layer of transparent shell (the inner prismatic layer) covers the venter between the longitudinal lines. There are a series of transverse lines on the dorsal side of each longitudinal line on both sides of the specimen. On the adoral portion of the specimen on the left side, the transverse lines are concave on the outer flanks and bend strongly forward toward the longitudinal line, meeting it almost asymptotically. They are regularly spaced at intervals of 1–2 mm, as measured along the longitudinal line. On the adapical portion of the specimen on the right side, the transverse lines are slightly

Fig. 15. Ventral view of *Menuites oralensis* Cobban and Kennedy, 1993, USNM 506948, part of a phragmocone of a macroconch (D = 114.0 mm), *Baculites scotti* Zone, Pierre Shale, South Dakota. There is a nearly continuous longitudinal line on the ventrolateral margin on each side of the specimen (left and right arrows). Several transverse lines occur on the venter (middle arrow). Adoral direction is toward top of photo. Approximately natural size.

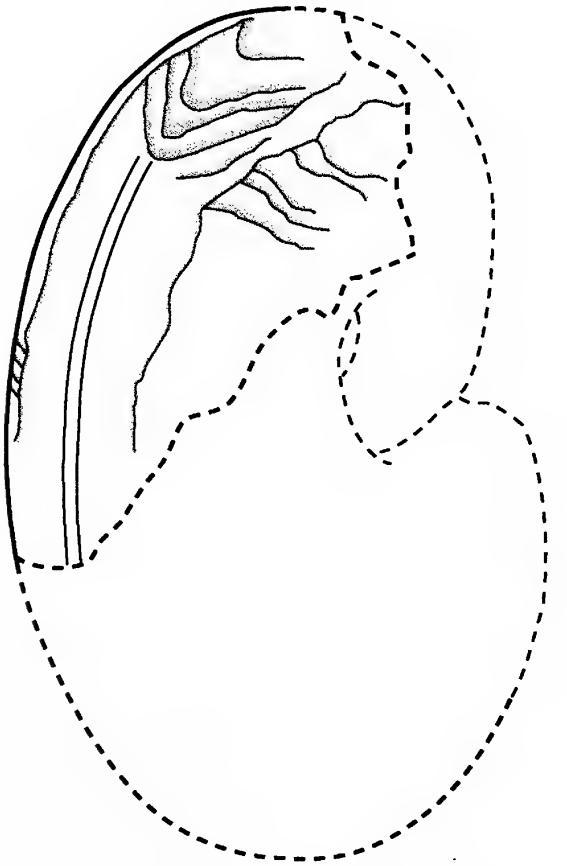

Fig. 16. Diagram of *Menuites oralensis* Cobban and Kennedy, 1993, *Baculites scotti* Zone, Pierre Shale, South Dakota. Three-quarter view of USNM 506948, part of a phragmocone of a macroconch (specimen in fig. 15), showing transverse lines, longitudinal lines, and the mid-ventral band. The dashed outline represents the missing portion of the specimen. ×0.90.

sinuous and intersect the longitudinal line at nearly right angles. All of the lines occur on a thin layer of transparent shell, the inner prismatic layer, and lie below the longitudinal line in terms of elevation. None of these transverse lines continues onto the venter. However, there are several other transverse lines on the venter, which are visible on the adapical portion of the specimen. These lines form a strong adoral projection, which is not as well defined as that in other specimens.

In An1086A, a specimen of *Pachydiscus* (*P.*) cf. *catarinae* (figs. 17, 18), there is a longitudinal band on the flanks that extends from the umbilicus to approximately one-half whorl height. The ventral margin of the band does not coincide with the position of the umbilical seam of the next (missing) whorl. The band occurs on a layer of transparent to opaque shell, presumably the inner prismatic layer. The ventral margin of the band is clearly defined on the adoral one-quarter whorl. This margin consists of several thin bands of nacre, 5 mm wide in total. These thin bands are stacked one on top of another in the dorsal direction. Each band is 1–2 mm wide and has a thick, ragged ventral edge and a feather-thin dorsal edge. On the other three-quarters of the whorl, the ventral margin of the longitudinal band is marked by the boundary between a region of thick nacreous shell on the outer half of the flanks and venter and a region of thin transparent-to-opaque shell on the inner half.

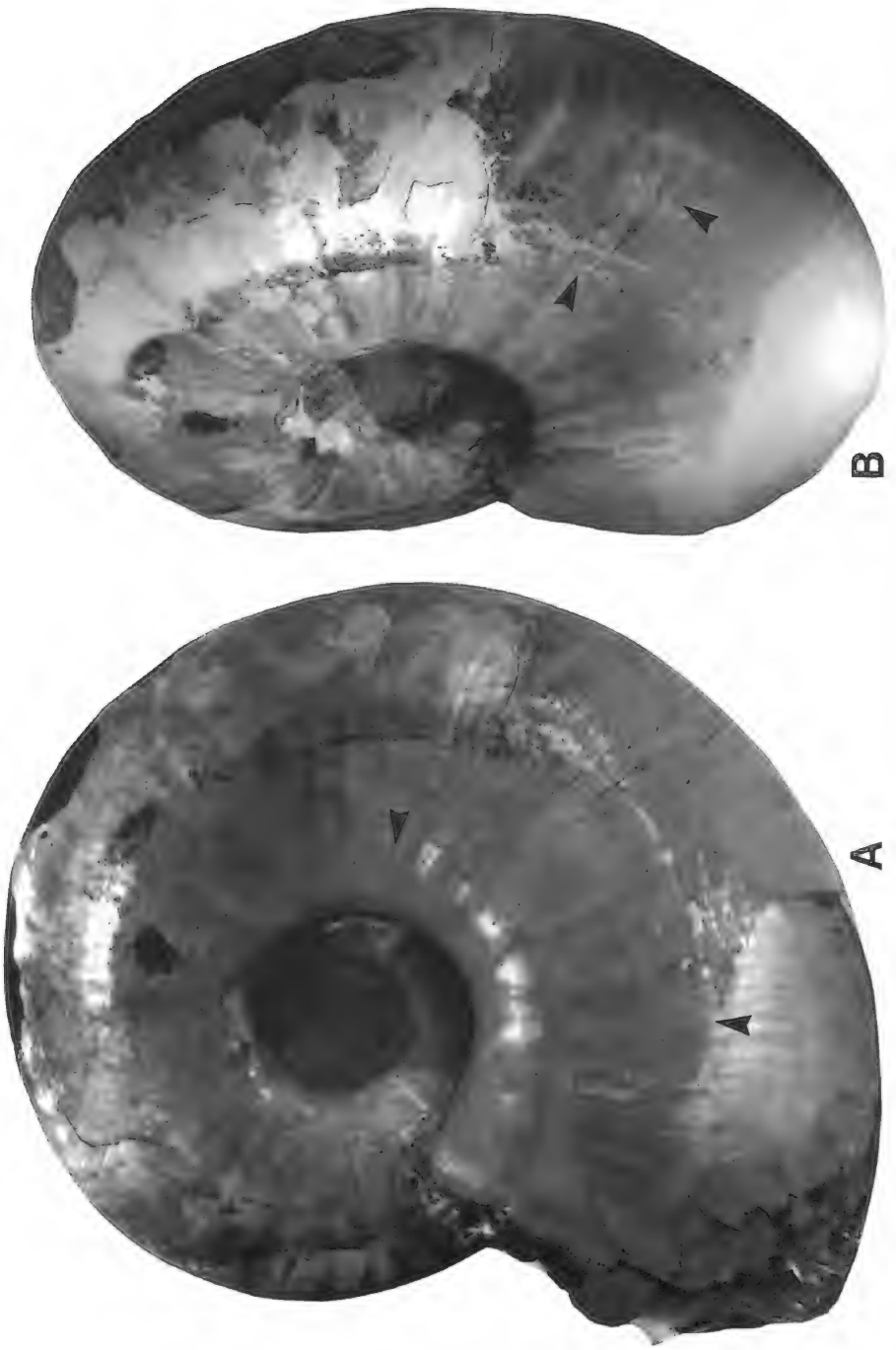

Fig. 17. *Pachydiscus* (*Pachydiscus*) cf. *catarinae* Anderson and Hanna, 1935, An1086A, a large phragmocone (D = 164 mm), *Baculites scotti* Zone, Pierre Shale, South Dakota. **A.** Left lateral view showing the ventral margin of the longitudinal band (lower arrow). A brownish longitudinal band (upper arrow) also occurs on the umbilical wall and inner flanks. ×0.75. **B.** Three-quarter view showing the ventral margin of the longitudinal band (upper arrow) and a series of transverse lines on the venter (lower arrow). ×0.75.

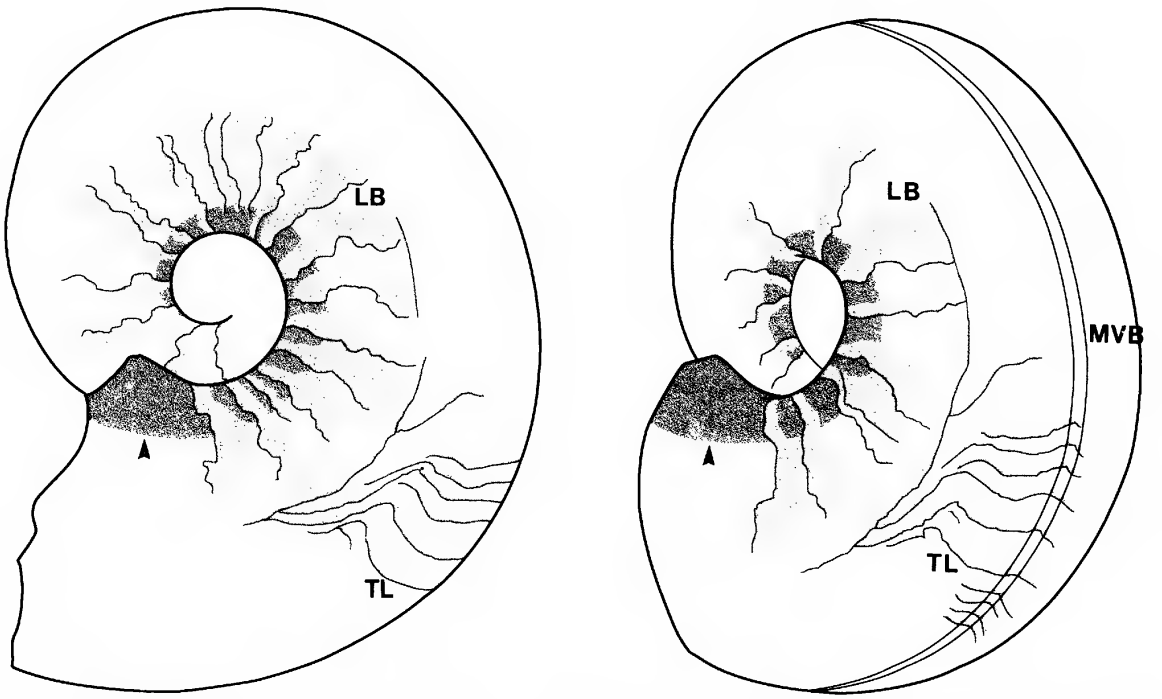

Fig. 18. *Pachydiscus* (*Pachydiscus*) cf. *catarinae* Anderson and Hanna, 1935, An1086A (specimen in fig. 17). Left lateral (left) and three quarter view (right) showing transverse lines (TL), the longitudinal band (LB), and the mid-ventral band (MVB). The transverse lines form a weak adapical projection on the venter, unlike other specimens in which there is an adoral projection. The arrow indicates a band of brownish color (darker shaded area) on the umbilical wall and inner flanks, which probably represents the trace of the dorsal scar. ×0.55.

The flanks of this specimen are covered by a series of thin sheets of nacre with each adapical sheet lying on top of the next most adoral sheet in an imbricated fashion. The adoral edge of each sheet is rursiradiate on the umbilical wall and approximately rectiradiate on the flanks. The adoral edge of each sheet is thick and extremely irregular, whereas the adapical edge feathers out and disappears. A few sheets extend the entire length from the umbilical seam to the ventral margin of the band. In most instances, only a narrow iridescent line (0.5 mm wide), not a broad sheet, is present near the umbilical seam. This line has a ragged adoral edge and a thin adapical edge.

On the ventral side of the longitudinal band there are a number of transverse iridescent lines. They appear on a layer of opaque shell, presumably the inner prismatic layer, and lie below the longitudinal band in terms of elevation. Each line is narrow, approximately 1 mm wide, and has a raised adoral edge and a feather-thin adapical edge. The lines bend sharply backward from the longitudinal band; they are broadly convex on the ventrolateral margin and weakly concave on the mid-venter. Each line is nestled within the margin of the preceding line. The lines are fairly regularly spaced at intervals of 5 to 10 mm, as measured on the mid-venter.

Summary

What we define as the longitudinal band is a layer of nacreous shell on the flanks that extends from the umbilicus to one-half to two-thirds whorl height. This feature is well developed on the body chambers of USNM 456679 and BHMNH 4811, both of which are macroconchs. The band occurs on the surface of the inner prismatic layer. In some areas, the band is thick and consists of a succession of nacreous layers stacked up in the

dorsal direction. Elsewhere, only the ventral margin of the band is visible. The ventral edge of this margin feathers out and disappears but the dorsal edge is thicker and more ragged. Commonly, there are patches of nacreous shell on the dorsal side of this margin. In USNM 456679, these patches appear as a series of transverse lines that are concave on the flanks and join the margin of the band almost asymptotically.

A longitudinal band is also visible in USNM 506948 and An1086A, both of which are phragmocones and subject to overprinting by later growth. In An1086A, the band is well developed and similar to that in USNM 456679. However, there are two differences: (1) the ventral edge is thick and ragged and the dorsal edge feathers out and disappears on the ventral margin of the band, the reverse of the situation in the other three specimens, and (2) the transverse lines on the venter form a weak adapical projection instead of an adoral one. In USNM 506948 only the ventral margin of the band is present and represents more of a line than a band.

MID-VENTRAL BAND

Observations

AMNH 46004, a large macroconch, shows a mid-ventral band, 6 mm wide, on the adapical part of the body chamber (figs. 4, 5). It extends for a distance of 47 mm adoral of the last suture (measured from the top of the first lateral saddle), although for the initial 22 mm, it is not preserved. The band is visible in places on the surface of the internal mold and in other places through a layer of transparent shell. It consists of two darker subbands that are the color of the matrix, with a yellowish subband in the middle although the boundaries between these subbands are irregular. The most adoral portion of the band is dark and ends abruptly. A narrower band, 2.5 mm wide, continues for almost another quarter whorl and consists of two yellowish subbands with a darker subband in the middle. It is visible through a layer of transparent shell.

In USNM 506947, a juvenile, the last septum is very thin and was probably in the process of formation at the time of death (fig. 6B). A mid-ventral band, 1.5 mm wide, extends 2 mm adoral of this septum. In some areas, the entire band is white but in most areas it is the color of the matrix and is outlined in white. It is visible through a very thin layer of transparent shell.

In Me590A, a microconch (D = 88.4 mm), there is a mid-ventral band on the phragmocone and adapical part of the body chamber, which is visible through a thin layer of transparent shell (figs. 12D, 19A). It extends approximately 30 mm adoral of the mid-ventral saddle of the last suture. It is yellowish in color with a narrow subband in the middle, which is lighter in some places and darker in others. The band is 2.5 mm wide on the body chamber and ends abruptly, although its outline is visible for another few millimeters. A narrower band, approximately 1.5 mm wide, extends from the right half of the original band. It consists of a light yellow line on each side and a dark matrix-colored line in the middle, extending for 34 mm, approximately one-fifth whorl.

In Me1088, a microconch, a mid-ventral band 3.5 mm wide extends approximately 10 mm adoral of the last suture (measured from the top of the first lateral saddle) (figs. 10A, 11). It is yellowish in color and is visible through a thin layer of transparent shell. A narrower band, 1.25 mm wide, extends from the center of the broader band. This narrow band consists of a darker-colored midline and lighter-colored lateral lines, and although the shell layer below which it lies becomes more opaque, the band is visible for 31 mm. The layer of shell is missing beyond this point and the band is expressed on the internal mold as a narrow ridge with grooves on either side. It continues for another 18 mm until there is a break in the specimen, about midway into the body chamber.

In USNM 506949, a small microconch (D = 67.7 mm), a white mid-ventral band extends 20.5 mm adoral of the ventral saddle of the last suture (fig. 2B) and is visible through a thin layer of transparent shell. The band is narrow (2 mm wide) between the lateral saddles of the last suture and then gradually flares out reaching a width of 3.5 mm. A thin (0.25 mm wide) white line in the middle of the band is outlined by darker matrix-colored patches on either side. The band ends abruptly in a sharp, irregular margin. How-

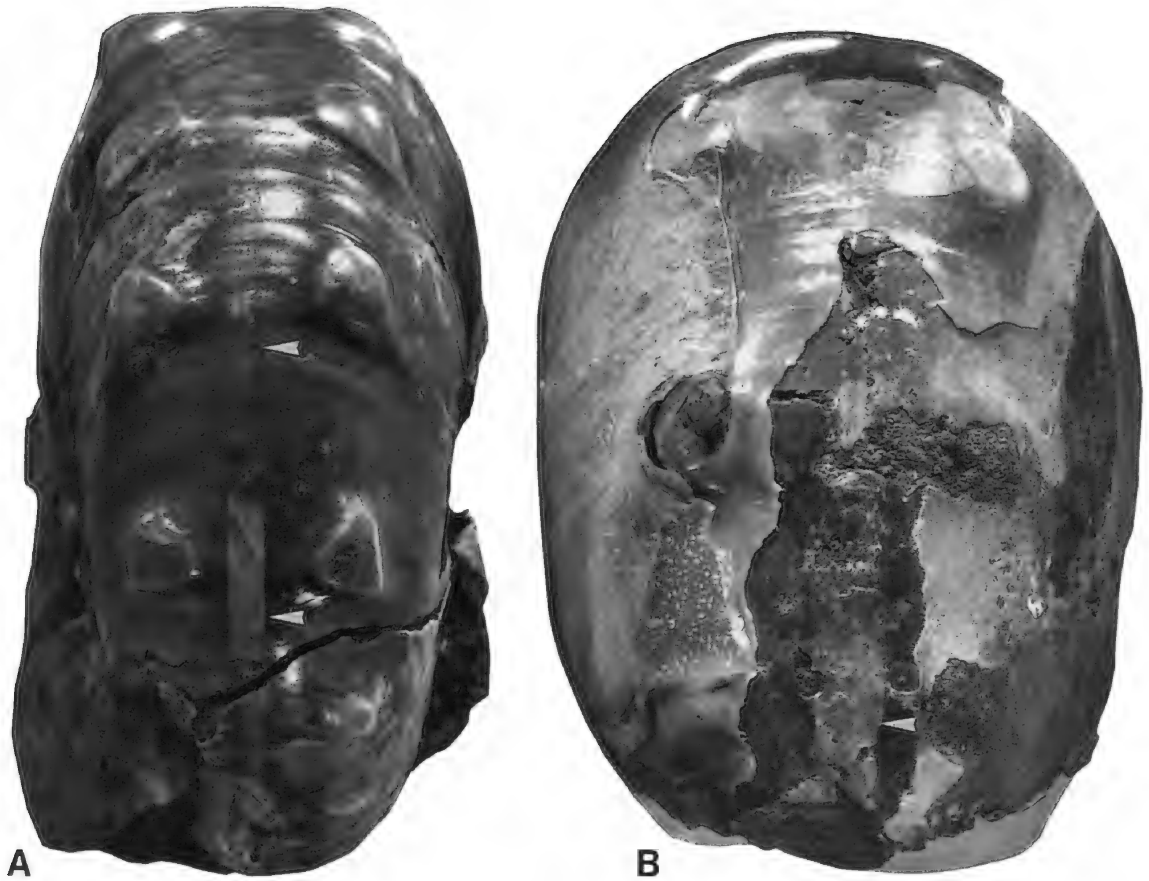

Fig. 19. *Menuites oralensis* Cobban and Kennedy, 1993, microconchs, *Baculites scotti* Zone, Pierre Shale, South Dakota. Ventral views of the adapical part of the body chamber showing the mid-ventral band. Adoral direction is toward top of photos. Uncoated. **A.** Me590A (specimen in fig. 12D). The mid-ventral band (lower arrow) is visible through a thin layer of transparent shell. It extends approximately 30 mm adoral of the last suture. It ends abruptly although the outline of the band continues for another few millimeters. A narrower band (upper arrow) extends from the right half of the original band and continues for an additional 34 mm. Approximately ×1.7. **B.** USNM 506951. The mid-ventral band (arrow) is visible on the internal mold (D = ~78 mm). It extends 14 mm adoral of the last suture and consists of a whitish band of shell, which is prismatic in microstructure (see fig. 1B). Approximately ×2.5.

ever, a narrower band (2 mm wide) continues for several millimeters more before it is covered by a thick layer of shell. It consists of two lighter lines on the outside and a darker line in the middle.

In USNM 506950, a macroconch (D = 87.8 mm), there is a mid-ventral band, 3.5 mm wide, that extends 32 mm adoral of the last suture (measured from the top of the first lateral saddle) (fig. 12B). This band is visible through a thin layer of transparent shell. It is whitish in color and only appears on the rib crests. A thinner band, 1.5–2 mm wide, continues thereafter for another 31 mm. It appears only on the rib crests and is whitish with a thin dark line in the middle.

In Me791, a microconch, there is a mid-ventral band, 3 mm wide, extending in an adoral direction from the base of the body chamber (fig. 10C). Initially, it is visible on the surface of the internal mold where it appears as a narrow band of whitish shell. Thereafter, it is visible through a thin layer of transparent shell. There is a thin, iridescent line in the middle of the band, which extends for 13 mm adoral of which the over-

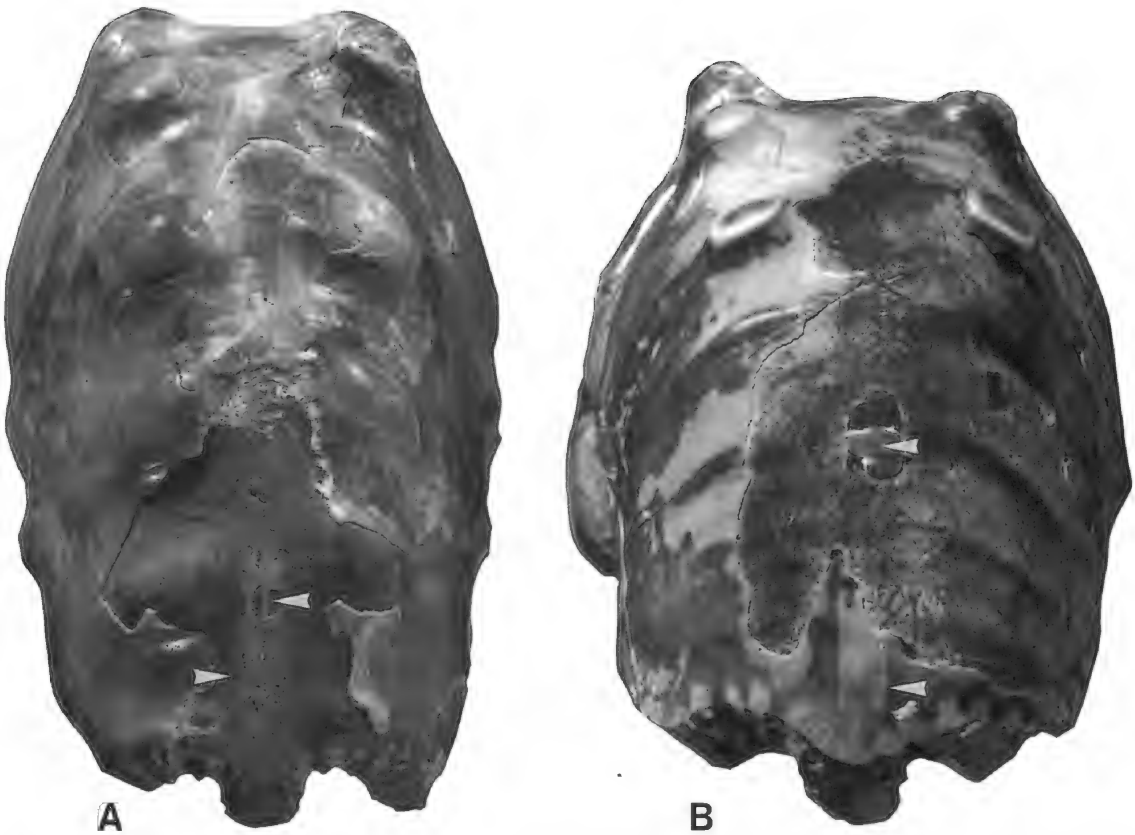

Fig. 20. *Menuites oralensis* Cobban and Kennedy, 1993, microconchs, *Baculites scotti* Zone, Pierre Shale, South Dakota. Ventral views of the adapical part of the body chamber showing the mid-ventral band and muscle scar. Adoral direction is toward top of photos. Uncoated. **A.** AMNH 46489 (specimen in fig. 10D). The mid-ventral band (left arrow) is visible on the internal mold. It extends 20 mm adoral of the last suture. It ends fairly abruptly although the outline of the band continues for an additional 2 mm. In some places, the band has eroded away, revealing a narrow central subband underneath (right arrow). Approximately ×1.75. **B.** BHMNH 4926. The mid-ventral band (lower arrow) extends 16 mm adoral of the last suture. It terminates in a raised oval area (upper arrow), which we interpret as the mid-ventral muscle scar. Approximately ×2.6.

lying layer of shell becomes opaque. This layer of shell is broken away in places revealing a narrow ridge on the mid-venter of the internal mold flanked by shallow grooves on either side. This feature extends for 23 mm until it is covered by a layer of shell.

The mid-ventral band is exposed on the internal mold of USNM 506951, a microconch (D = ~78 mm) (figs. 1B, 19B). It extends 14 mm adoral of the last septum and consists of a whitish band of shell, 3 mm wide and 40 μm thick. It is prismatic in microstructure.

In AMNH 46489, a microconch, there is a mid-ventral band, 3.5 mm wide, that extends 20 mm adoral of the base of the body chamber (figs. 10D, 20A). It is visible on the internal mold where it appears as a layer of whitish shell with a weak ridge along the midline, flanked by shallow grooves on either side. The band ends fairly abruptly, although its outline continues for an additional 2 mm. In some places, the band has eroded away, revealing a narrow, central subband of whitish shell, 0.5 mm wide, underneath. This subband is flanked by shallow grooves on either side on the internal mold. Several millimeters adoral of the end of the broad mid-ventral band, the internal mold is covered by a layer of transparent shell. Below this layer,

a narrower band, 2.5 mm wide, is visible. This brownish-colored band lies along the midline and shows two thin white lines in the middle. It extends for 13 mm, adoral of which the layer of shell is missing.

BHMNH 4926, the body chamber of a small microconch, shows the mid-ventral band terminating in a scar (fig. 20B). The band extends 16 mm adoral of the last septum (measured from the top of the first lateral saddle). For the initial 7 mm, the whitish band is visible below the inner prismatic layer. Thereafter, it appears as a dark band on the internal mold. It terminates in a raised oval area, 4.5 mm long. Part of this area is covered by the inner prismatic layer. We interpret this feature as the mid-ventral scar.

Summary

There is a mid-ventral band on the phragmocone and adapical part of the body chamber. To avoid any possible confusion due to overprinting from later growth, we focus on the body chamber. Our observations reveal that there are two different but related bands.

(1) There is a broad mid-ventral band that extends adoral of the last septum. It ranges from 1.5 mm wide in a small juvenile (USNM 506947) to 6 mm wide in a large macroconch (AMNH 46004). In most adult specimens, it ranges from 2.5 to 3.5 mm wide. It extends 10–30 mm adoral of the last septum, except in AMNH 46004 in which it extends 47 mm. The whitish to yellowish band is visible through a thin layer of transparent shell (the inner prismatic layer). It is a solid band in Me1088, Me791, and USNM 506950 and 506951. In contrast, in Me590A, there is a subband in the middle that is lighter in some places and darker in others. In AMNH 46004, there are two darker subbands on the outside with a lighter subband in the middle. The mid-ventral band is also exposed on the surface of the internal mold without the overlying inner prismatic layer present. In AMNH 46489, the band appears as a strip of whitish to yellowish shell with a weak ridge in the middle and shallow grooves on either side. There is a narrow, central subband of whitish shell underneath. This subband is flanked by shallow grooves on either side on the internal mold. In most specimens, the mid-ventral band ends fairly abruptly, although its outline generally continues another few millimeters (e.g., in Me590A). The band terminates in an unpaired muscle scar.

(2) There is a narrow mid-ventral band that continues adoral of the broad band. This narrow band ranges from 1.25 to 2.5 mm in width, representing approximately 40–70% of the width of the broad band. The narrow band extends much farther than the broad band (e.g., 0.2 whorls in Me590A and 0.25 whorls in AMNH 46004) and terminates in the middle of the adult body chamber. In four specimens (AMNH 46004, Me590A, Me1088, and USNM 506949) it is present at the adoral end of the broad band, and may, in part, represent a continuation of it. The narrow band extends from the *middle* of the broad band except in Me590A in which it extends from the *right half* of the broad band. It is visible through a thin layer of transparent shell (the inner prismatic layer) and usually consists of two light-colored subbands with a darker subband in the middle. The band is expressed on the internal mold as a narrow ridge with grooves on either side (e.g., in Me1088).

DORSAL SCAR

Observations

In BHMNH 4923, an adult microconch, there is a narrow transverse band on the umbilical wall on the right side of the body chamber (fig. 7D). It is 1.5 mm adoral of the ultimate septum. The band is cream colored with two lighter lines on the outside and a darker line in the middle. It is visible through a layer of transparent shell and is 0.5 mm wide at the umbilical seam. The band is prorsiradiate and weakly convex on the inner part of the umbilical wall and prorsiradiate and weakly concave on the outer part. It is 0.8 mm wide at its widest point. Part of the band peels off just dorsal of the umbilical shoulder and extends forward for 1 mm; it then turns toward the umbilical seam, forming a small lobe. The main part of the band continues to the umbilical shoulder, narrowing to a width of 0.25 mm; it then curves forward for about 2 mm before it disappears. Adapical of the band, the umbilical wall is slightly lighter

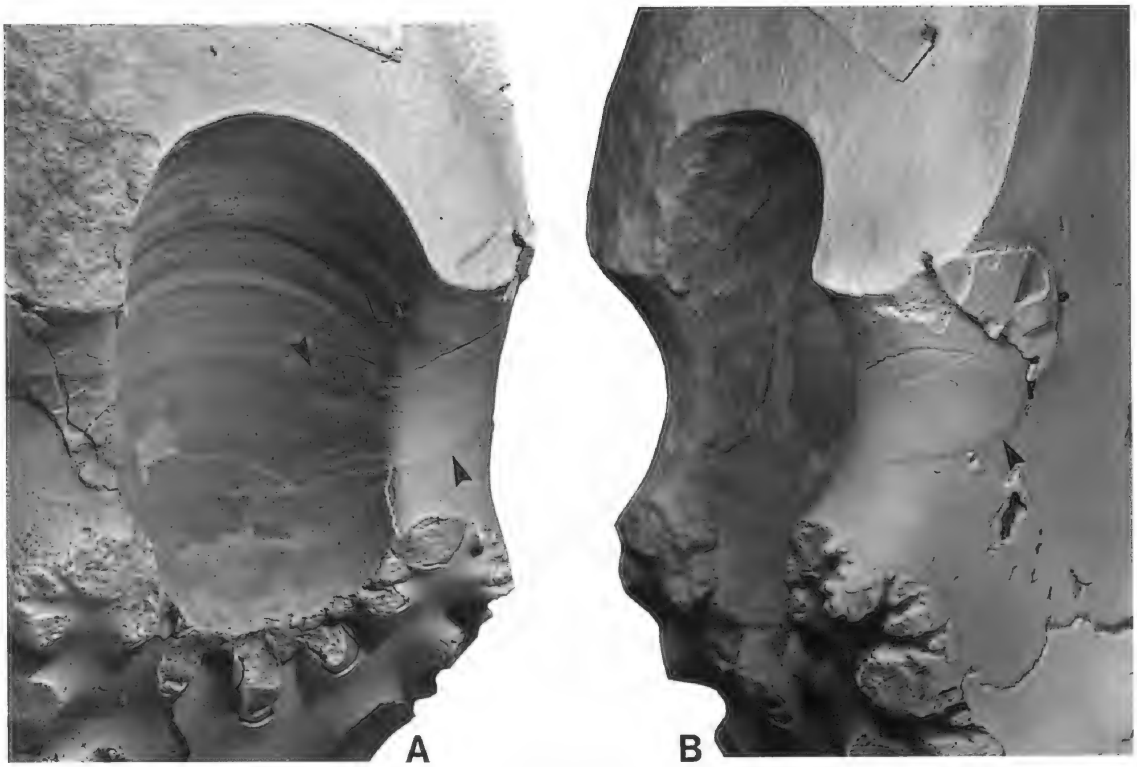

Fig. 21. Dorsal muscle scar in *Menuites oralensis* Cobban and Kennedy, 1993, USNM 506952, an internal mold of part of the body chamber of a microconch, *Baculites scotti* Zone, Pierre Shale, South Dakota. **(A)** dorsal view; **(B)** right lateral view. The muscle scar (arrows) is boomerang-shaped and extends from the dorsal margin (left photo) to just ventral of the umbilical shoulder (right photo). Coated, approximately ×2.5.

than the flanks but adoral of the band, it is slightly darker. These patterns are visible through a thin layer of transparent shell.

In Me590A, an adult microconch, there is a narrow yellowish transverse band on the umbilical wall on the right side of the body chamber. It is approximately 5 mm adoral of the ultimate septum, as measured along the umbilical seam, and is visible through a thin layer of transparent shell. It is prorsiradiate and slightly sinuous on the umbilical wall with a maximum width of 1 mm. It narrows down to a thin line at the umbilical shoulder, and then arches forward for about 4 mm, after which there is a break in the specimen.

In USNM 506949, an adult microconch, there is a thin transverse band on the umbilical wall on the right side of the body chamber just adoral of the ultimate septum. The band is whitish and is visible through a thin layer of transparent shell. It is narrow (0.5 mm wide), straight, and rectiradiate on the inner part of the umbilical wall. It is broader (1.5 mm wide), concave, and prorsiradiate on the outer part of the umbilical wall and shoulder. The band extends outward for approximately 9 mm after which there is a break in the specimen.

USNM 506952, a microconch (figs. 21, 22) has the best muscle scar. It occurs on each side of the body chamber but is much better defined on the right side. It is visible on the internal mold and is not covered by any shell layers. It is 3 mm adoral of the ultimate septum, as measured along the umbilical seam. The scar has a boomeranglike shape and extends from the dorsal margin to just ventral of the umbilical shoulder. It is not continuous across the dorsum. It is relatively large, attaining a maximum width of 5.5 mm on the umbilical shoulder. The edge of the scar on the flanks (the ventral margin) is de-

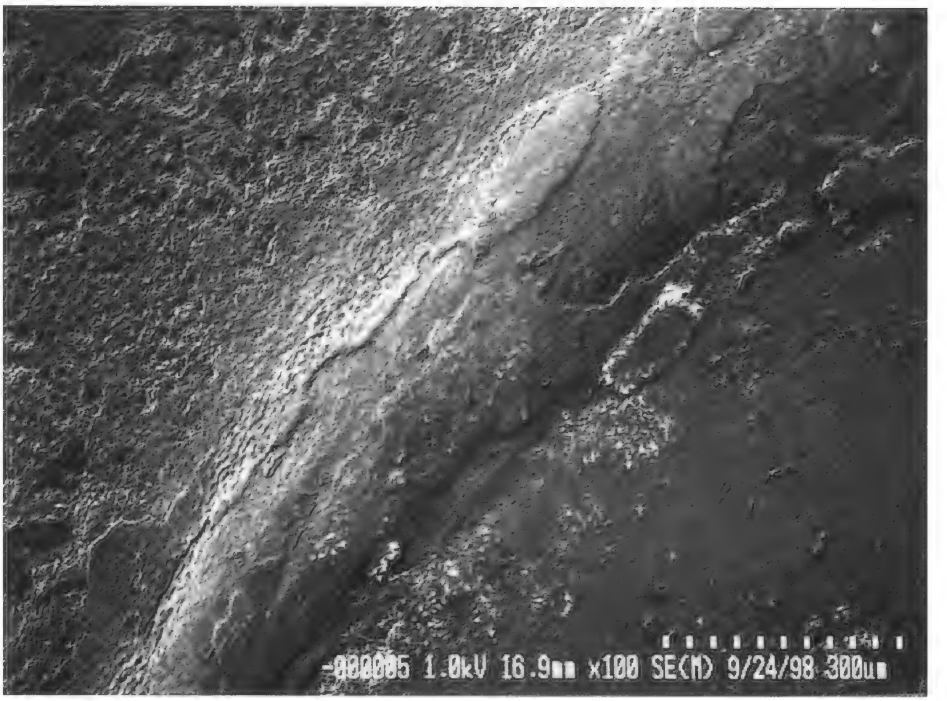

Fig. 22. Close-up of the rim of the dorsal muscle scar in *Menuites oralensis* Cobban and Kennedy, 1993, USNM 506952 (specimen in fig. 21). The edge of the scar is demarcated by a series of ridges and grooves, reflecting the relief on the inside surface of the body chamber. (The location of this photo is shown by the arrow in fig. 21B, rotated 180°.) Scale indication = 300 μm.

marcated by a series of ridges and grooves, reminiscent of an eroded anticline. The following features are present from the outside of the edge toward the inside: (1) a groove, (2) a ridge that dips away from the center of the scar, (3) a groove, (4) a ridge that dips in the same direction as the outer ridge but at a lesser angle, (5) a very small groove, and (6) a saddlelike depression (the surface of the scar itself). Features 1, 2, and 3 are also present on the adapical margin of the scar but 1 is stronger and 2 and 3 are weaker than on the ventral margin. Only the groove (3) inside the outer ridge is present on the dorsal and adoral margins of the scar. A small ridge extends backward from the muscle scar along the umbilical shoulder for about 2 mm.

BHMNH 4926, a microconch, shows part of a dorsal scar on the left side of the body chamber. It occurs on the internal mold about 3–4 mm adoral of the ultimate septum, as measured along the umbilical seam. Only the portion of the scar on the dorsum and umbilical wall is preserved. The scar extends only a short distance onto the dorsum compared to USNM 506952.

The trace of the dorsal scar appears in An1086A, a large phragmocone that retains several layers of shell, some of which are transparent (figs. 17, 18). A longitudinal band on the left side of the specimen extends from the umbilical seam to the inner part of the flanks. It is faint on the adapical quarter of the whorl, conspicuous on the rest of the whorl, brownish, and visible through a layer of transparent shell. The margin of the band is sharply defined and highlighted in places by a thin brown line. The band does not coincide with any shell layer on the surface. It is possible that the margin of the band marks the umbilical seam of the next (missing) whorl. Unfortunately, the band is very faint on the adapical part of the whorl where it would have been easiest to trace the continuation of the umbilical seam. However, there is no residual material along the margin that would indicate the attachment of the next

whorl. We prefer to interpret this band as the trace of the dorsal scar.

SUMMARY

These specimens indicate the presence of a pair of dorsal muscle scars just adoral of the ultimate septum. In BHMNH 4923, Me590A, and USNM 506949 there is a narrow transverse band on the umbilical wall, which is visible through a thin layer of transparent shell and represents the shell material (myostracum) on the adapical margin of the muscle scar. The muscle scar is preserved on the internal mold in USNM 506952 and BHMNH 4926. In USNM 506952 it is boomerang-shaped and extends from the dorsal margin to just ventral of the umbilical shoulder. The edge of the scar is demarcated by a series of ridges and grooves, reflecting the relief on the inside surface of the body chamber. In An1086A, there is a brownish longitudinal band on the umbilical wall and inner flanks of the phragmocone. This band is visible through a layer of transparent shell and represents the trace of successive sites of the dorsal muscle scar.

DISCUSSION

There are four main features on these specimens of *Menuites oralensis* and *Menuites portlocki complexus.* Most show transverse lines, which are thin iridescent bands of nacre that extend as far adorally as the middle of the body chamber. They appear on the venter, flanks, and umbilical wall. They may also occur on the dorsum, but there are no suitable specimens to document this. The transverse lines are sinuous and prorsiradiate on the flanks. In most specimens, they cross the venter with a sharp adoral projection, forming a series of closely spaced chevrons. They occur on the surface of the inner prismatic layer.

Fewer specimens show a longitudinal band, which occurs on the surface of the inner prismatic layer and extends from the umbilicus to one-half to two-thirds whorl height. It appears as a series of nacreous layers that are stacked up in the dorsal direction on the phragmocone and body chamber. In most specimens, the ventral margin of the band feathers out and disappears.

The other features we observed are located in the adapical part of the body chamber. A mid-ventral band extends adoral of the last septum. It consists of a layer of shell, several millimeters wide, that is visible below the inner prismatic layer. It extends 10–30 mm adoral of the last septum in most adult specimens and terminates in an oval mid-ventral scar. A narrower band continues adoral of the first band and extends to the middle of the body chamber. It appears on the internal mold as a narrow ridge flanked by grooves on either side.

A pair of dorsal muscle scars is also present in the adapical part of the body chamber. They are boomerang-shaped and extend from the dorsal margin to just ventral of the umbilical shoulder. In a few specimens, the layer of shell (myostracum) on the scar is visible on the internal mold. One specimen shows a brownish longitudinal band visible below the inner prismatic layer on the umbilical wall and inner flanks of the phragmocone, which probably represents the trace of the successive sites of dorsal muscle attachment.

Several of these features have been reported elsewhere. Paired dorsal muscle scars are common in many ammonoids (Jordan, 1968; Doguzhaeva and Mutvei, 1996; Sarikadze et al., 1990). Rakus (1978) defined two forms of scars, one in which the entire outline of the scar is visible ("*type fermé*") and one in which only the adoral margin is preserved ("*type ouvert*"). According to this classification, the scar in *Menuites oralensis* is the "*type fermé.*" Jordan (1968) described several specimens of Jurassic ammonoids that preserved the trace of the dorsal muscle scar on the phragmocone, and he referred to this feature as the "*helles Schalen Band*" or the "*dunkeles Band,*" depending on its color. The latter band is identical to the brownish longitudinal band on the umbilical wall and inner flanks of the phragmocone of An1086A. The dorsal muscle scar has generally been interpreted as the site of attachment of the cephalic retractor muscles (Doguzhaeva and Mutvei, 1996).

The mid-ventral scar is also well known and has been called the "unpaired ventral attachment scar" by Doguzhaeva and Mutvei (1996). These authors interpreted it as the site of attachment of a muscle or ligament

that maintained the position and shape of the circumsiphonal invagination at the adapical end of the body.

Less well known is the broad mid-ventral band that extends adoral of the last septum and terminates in the mid-ventral scar. Jordan (1968: 32) illustrated a few specimens in which this feature appears as a black band in the adapical portion of the body chamber. Henderson (1984: pl. 49, fig. 5) also illustrated an example of this band on the internal mold of a body chamber of a lytoceratid. This band has been well documented on phragmocones and has recently been described in detail on the phragmocones of goniatites (Tanabe et al., 1998). The presence of this band in the body chamber is probably related to the fact that the siphuncular tube (=connecting ring) extended into the adapical part of the body chamber. This phenomenon has been observed in several ammonites (Druschits and Doguzhaeva, 1974: fig. 2; Kulicki, 1979: pl. 40, fig. 1; Westermann, 1982: fig. 3; Doguzhaeva, 1988: fig. 2).

The narrow mid-ventral band that continues into the body chamber adoral of the mid-ventral scar has also been reported in many ammonoids. For example, Landman and Waage (1993: fig. 153G) documented it on the internal molds of scaphites. They described it as "a very faint, low rounded ridge that runs along the mid-venter from the ventral muscle attachment area nearly to the aperture" (ibid.: 46). Jones (1967: pl. 2, figs. 12, 18) illustrated this feature on internal molds of tetragonitids. A similar, if not identical, feature has been recognized in nautiloids where it has been called the "conchal furrow" (Teichert, 1964). This feature is expressed on the inside surface of the shell wall as a groove flanked by narrow ridges and probably represents the impression of an internal organ.

In contrast, there are no reports of the transverse lines and the longitudinal band in other ammonoids. The closest known feature is the lateral sinus, which has been documented in Phylloceratina, Lytoceratina, and Ammonitina, including Desmoceratacea ("*Einbuchtung,*" Jordan, 1968; "*Abdruck des vorderen Lateralmuskelns,*" Sarikadze et al., 1990; Doguzhaeva and Mutvei, 1996). This feature is visible on the internal mold of the body chamber and appears as a sinus with an adoral opening. However, the lateral sinus differs from the transverse lines in that it does not cross the venter. It differs from the longitudinal band in that it does not extend to the umbilicus.

The transverse lines and the longitudinal band also bear some resemblance to the ventrolateral muscle scars described by Doguzhaeva and Mutvei (1991) in the Jurassic ammonite *Aconeceras trautscholdi* Sinzow, 1870. These scars form a prominent adorally directed lobe on the internal mold of the body chamber. In a few specimens, the entire surface of the scar is demarcated by shell material (ibid.: pl. 7, fig. 3; pl. 8, figs. 2, 3). More commonly, however, only the outline of the scar is present and consists of an iridescent rim of nacre (ibid.: pl. 3, figs. 1, 2; pl. 4, figs. 1, 2). The outer edge of this rim is feather thin and disappears, whereas the inner edge is thicker and more ragged. According to Doguzhaeva and Mutvei (1991: 20), this rim represents a remnant of the shell material that originally covered the entire surface of the scar.

The shape of these scars is completely different from that of the transverse lines and longitudinal band. However, the morphology of the rim along the margins of the ventrolateral scars may reflect a general pattern characteristic of sites of soft body attachment. The morphology of this rim is nearly identical to that of the transverse lines and the ventral margin of the longitudinal band in our specimens. The transverse lines are characterized by feather-thin adapical edges and more ragged, thicker adoral edges. Similarly, the ventral margin of the longitudinal band usually consists of a smooth, even ventral edge and a more ragged, thicker dorsal edge. The implication is that such features mark the boundaries of areas of nacreous secretion that extended in the direction of the broken edge.

Inspection of a specimen of *Aconeceras trautscholdi* (BHMNH 4934) (D = 43.7 mm) (fig. 23) revealed another feature very similar to the transverse lines in *Menuites oralensis.* This feature is illustrated by Doguzhaeva and Mutvei (1991: pl. 3, fig. 2; pl. 5, fig. 2) but not described by them. It consists of a series of iridescent lines on the internal mold of the

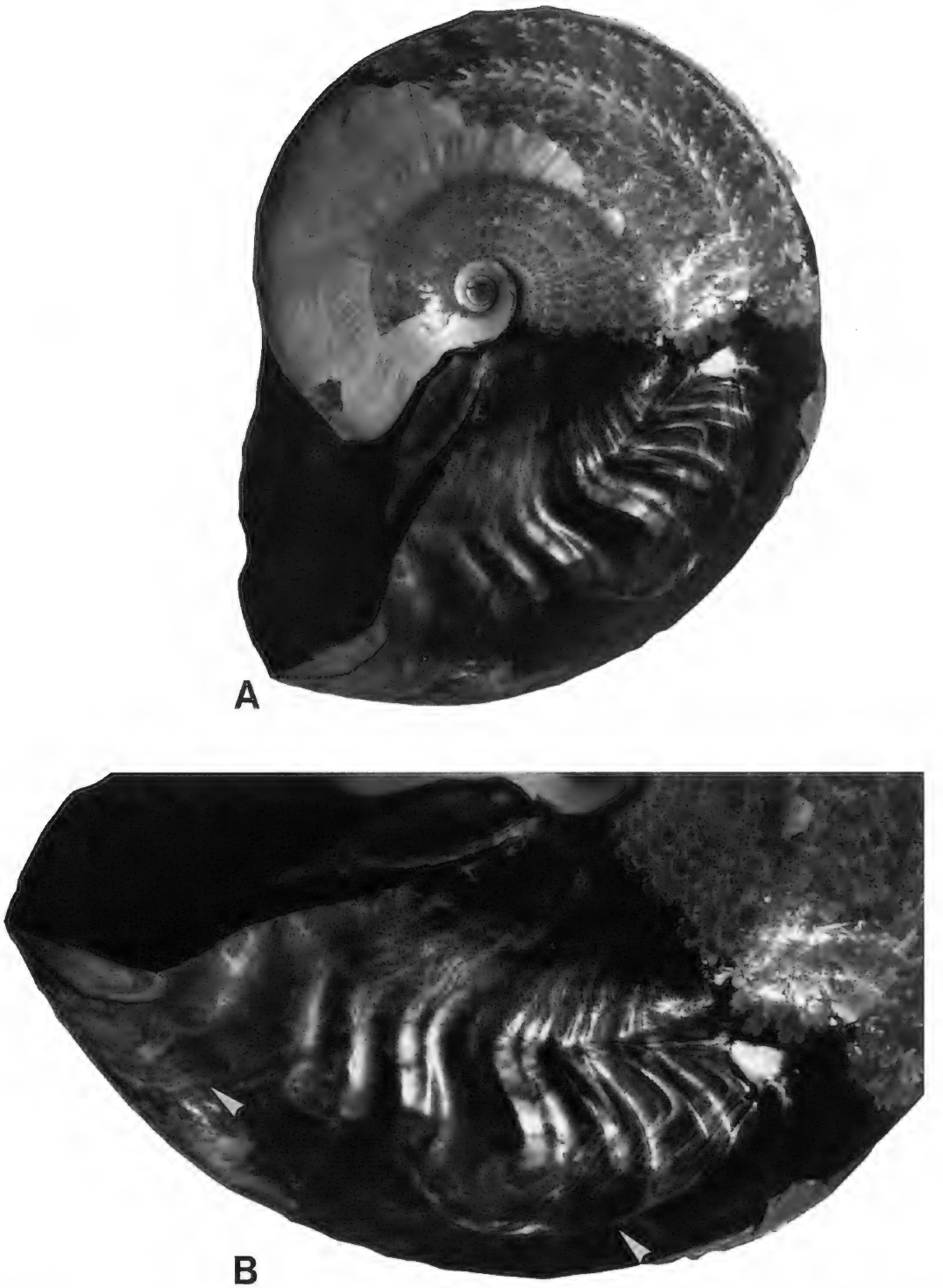

Fig. 23. *Aconeceras trautscholdi* Sinzow, 1870, BHMNH 4934, Aptian, Volga River, Russia (D = 43.7 mm). Uncoated. **A.** Left lateral view. The body chamber of the specimen is covered by the inner prismatic layer. Approximately ×2.0. **B.** Close-up of the body chamber showing transverse lines (left arrow), which follow the shape of the apertural margin, and the ventrolateral muscle scar (right arrow). Approximately ×3.5.

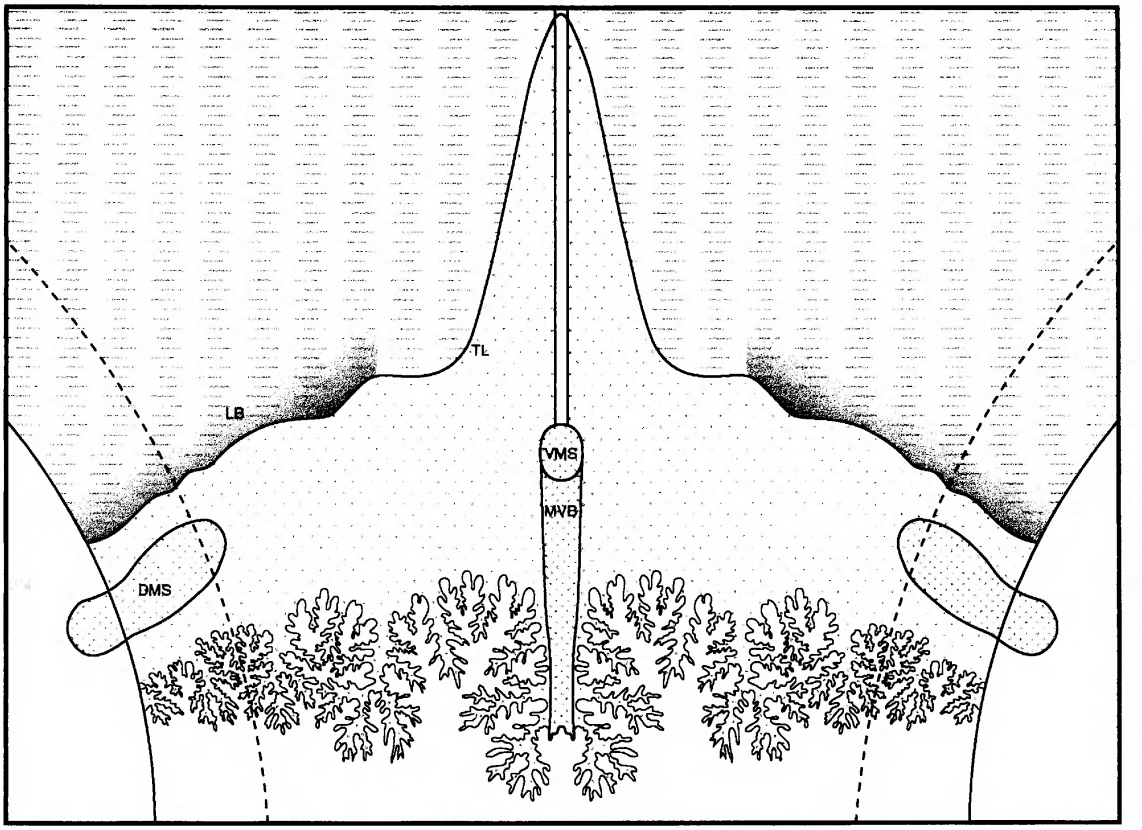

Fig. 24. Flattened representation of the inside surface of the body chamber of *Menuites oralensis* Cobban and Kennedy, 1993 showing dorsal muscle scars (DMS), mid-ventral band (MVB), ventral muscle scar (VMS), longitudinal band (LB), and transverse line (TL). The dots represent areas of prismatic secretion; the dashes, areas of nacreous secretion. Adoral direction is toward top of drawing. The dashed line represents the umbilical shoulder; the solid line, the umbilical seam. The microstructure of the dorsal area is not shown.

body chamber. These lines occur on a layer of transparent shell, presumably the inner prismatic layer. In BHMNH 4934, the lines are visible on the dorsal side of the ventrolateral muscle scar, and on the flanks and venter adoral of this scar. They are not present on the scar itself. The lines are prorsiradiate and sinuous on the flanks and cross the venter with a sharp adoral projection. On higher magnification, these lines appear as bands of nacre with feather-thin adapical edges and ragged adoral edges. The bands are narrow (0.25 mm wide) and closely spaced (4 lines/mm). However, unlike the transverse lines in *M. oralensis,* they follow the shape of the apertural margin, which consists of a rostral projection on the venter and a triangular lappet on the flanks.

These observations suggest that the transverse lines in all of these ammonites probably formed at the adapical margin of the zone of nacreous secretion in the middle of the body chamber. In *Aconeceras trautscholdi,* the shape of this margin was identical to that of the apertural margin. In contrast, in *Menuites oralensis* (and *Menuites portlocki complexus*), the shape of the adapical margin of this zone differed from that of the apertural margin (fig. 24). The transverse lines may have represented narrow bands of weak mantle attachment. The fact that they are closely and evenly spaced suggests incremental steps in the forward movement of the soft body. During the growth of the animal, the transverse lines were overlain by the inner prismatic layer. They are therefore now visible

on the surface of this layer on partially exfoliated shells.

The longitudinal band is more difficult to interpret. It demarcates an area of nacreous secretion on the flanks, probably in the middle of the body chamber adoral of the transverse lines (fig. 24). It may have represented an additional site of weak mantle attachment. Like the transverse lines, it was overlain by the inner prismatic layer during subsequent growth.

Thus, these specimens of *Menuites oralensis* (and *Menuites portlocki complexus*) show two areas of soft body attachment (fig. 24): (1) probably a weak area of attachment in the middle of the body chamber as represented by the transverse lines and the longitudinal band, and (2) probably a stronger area of attachment in the adapical part of the body chamber as represented by the mid-ventral band and scar and the pair of dorsal muscle scars.

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